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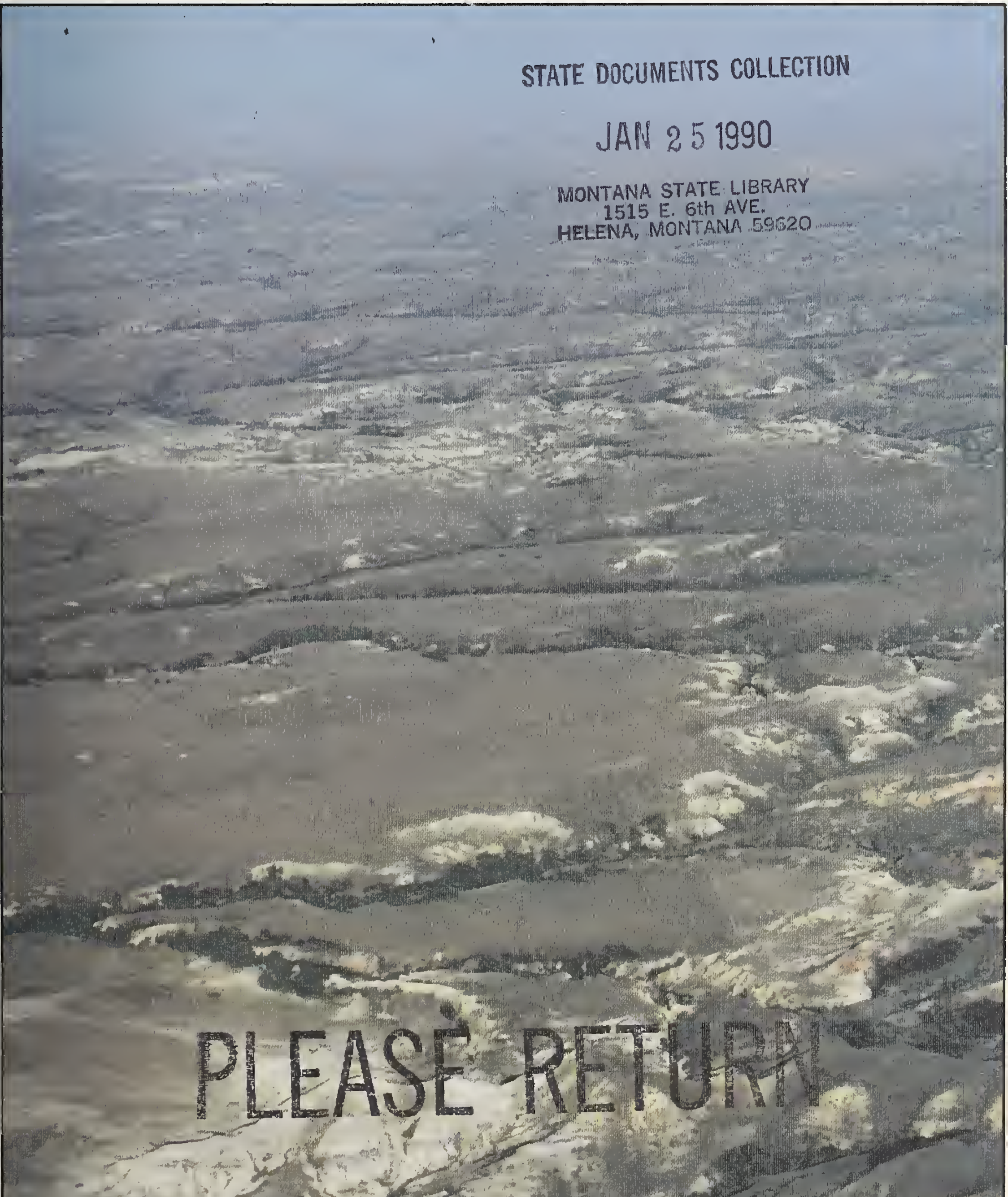

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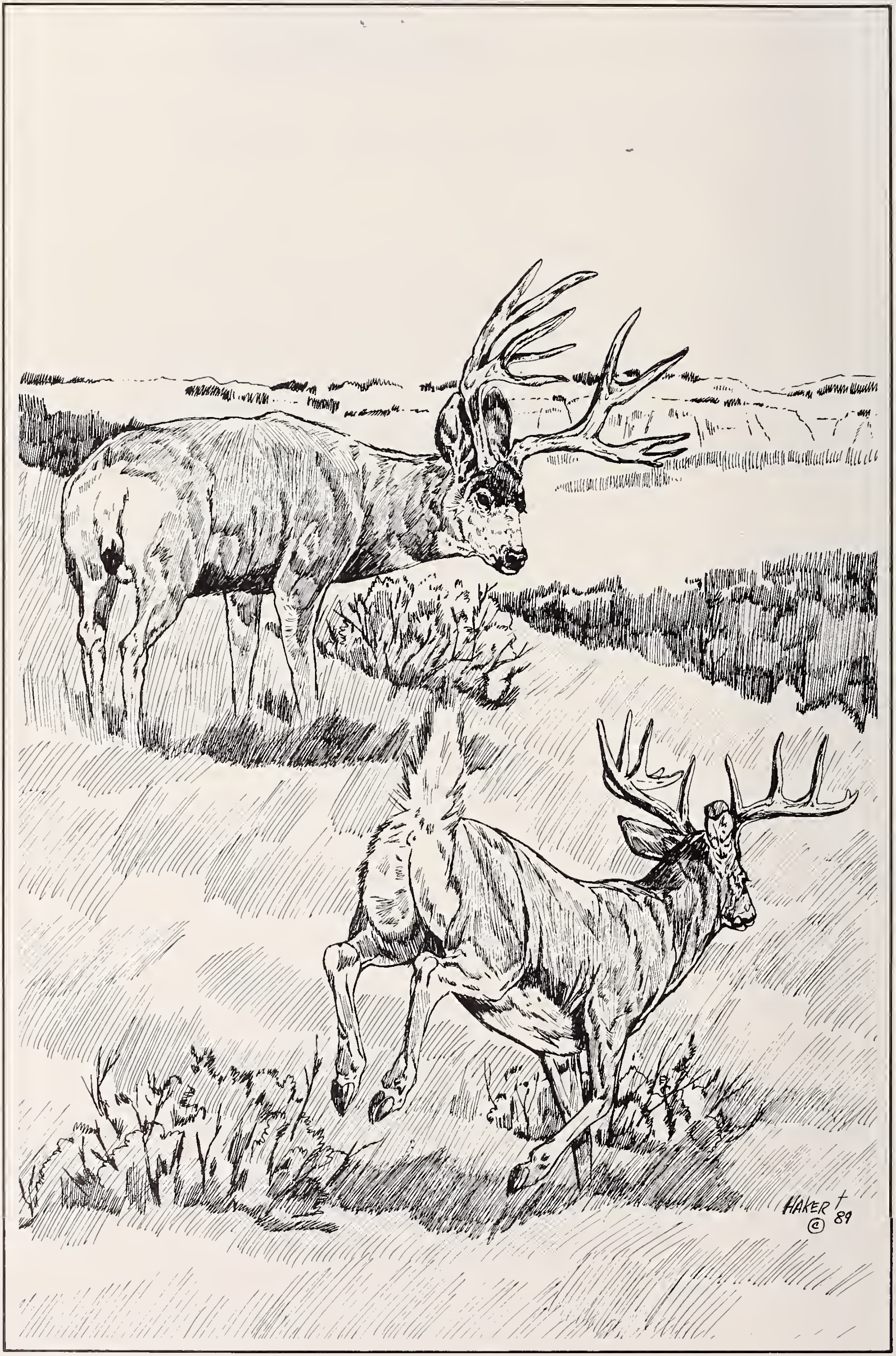
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ECOLOGY OF SYMPATRIC POPULATIONS OF MULE DEER AND WHITE-TAILED DEER IN A PRAIRIE ENVIRONMENT

by

Alan K. Wood, Richard J. Mackie and Kenneth L. Hamlin

Wildlife Division
Montana Department of Fish, Wildlife & Parks

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FOREWORD

Prairie. A place, a word that means a relatively flat or slightly undulating area characterized by low precipitation, dominated by grasses, and having deep, fertile soils. It's scarcity of trees and openness is explicit. The term "prairie," however, does not accurately reflect it's composite of many different, sometimes not so subtle, landforms and vegetation communities.

Prairie environments can be hot and dry in summer and bitter cold in winter; both extremes are often accentuated by wind. They are indeed semi-arid, with micro-environments ranging from dry to mesic. Wildlife that inhabits the prairie must acquire all of its needs from very small areas, or be capable of utilizing a variety of habitat units over a wide area.

Mule deer and white-tailed deer have evolved as inhabitants of the prairie. Like their environment, both species exhibit population dynamics and strategies that are much more complex that one might expect. Both species utilize the prairie differently, yet they coexist.

Man has also chosen the prairie as an inhabitable environment. Livestock grazing and cultivation of small grains and hay accompanied this settlement. Mule deer and white-tailed deer have adapted to these land uses, though the latter has probably benefitted more than the former.

The current report relates to a 12-year evaluation of the ecology of deer on prairies in eastern Montana. Deer populations were as variable as the prairie environment they occupied. Mule deer numbers increased 600% in eight years, while those of whitetails increased almost 250% in five years! Rates of increase of this magnitude have caused problems for ranchers and farmers. Numbers of deer declined just as dramatically. Mule deer numbers dropped 68% and whitetails 91% in four years! These decreases generated alarm by hunters and landowners.

Hunting was shown to be an effective tool in reducing numbers of both species in this environment. Fine-tuning hunting regulations to balance the desires of hunters with those of landowners remains part of the art of deer management on Montana prairies.

John P. Weigand

John P. Weigand
Chief, Research and
Technical Services Bureau

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SUMMARY

The ecology of sympatric mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) populations inhabiting a 543 km^2 eastern Montana prairie was studied during 1975-1987. Estimated spring populations of mule deer increased from approximately 180 in 1976 to 1,083 in 1983, stabilized during 1983-1984, and declined to 347 by 1987. Spring populations of whitetails declined from an estimated 200 deer in 1976 to about 135 in 1978, increased to approximately 335 in 1983, and subsequently declined to about 30 in 1987.

Populations fluctuated between seasons and years in relation to fawn and adult survival rates. Initial fawn production appeared to be relatively high in both species during most years, but survival varied considerably. Percent fawns in winter and spring populations was positively correlated with total precipitation from July through April prior to fawning, indicating that summer range condition was an important factor determining fawn survival and recruitment in both species.

Hunting was the major mortality factor among adults. Natural mortality rates among fawns and adults were not affected by population density. High deer numbers during 1982-1984 resulted in liberal hunting regulations and high hunting mortality. Harvest rates for mule deer averaged 21% for adult females and 58% for adult males during 1982-1986. The average for white-tailed deer during 1982-1985 was 31% for both adult females and adult males. Increased harvest rates combined with reduced fawn survival, appeared to be the major factors influencing population declines in both species during 1984-1987. Other mortality factors including winter severity, predation, and disease had relatively minor or highly variable effects on population trends and dynamics during the study.

On an annual basis, mule deer were distributed across only 32% of the study area, preferring areas of topographic diversity during winter and mesic vegetation during summer. Interspersion of habitat complexes containing those elements influenced seasonal movements, distribution, and home range size. Movements of adult females were characterized by three patterns that included yearlong residence (29%), summer migration (52%), and autumn migration (19%). Home range sizes of females varied from 0.5 to 19.7 km^2 during winter and from 0.5 to 6.2 km^2 in summer, depending upon local habitat characteristics and movement pattern followed. Overall, female mule deer demonstrated high fidelity to traditional herd ranges. Aggregations associated with specific herd range-habitat complexes appeared to comprise discrete subpopulation units.

White-tailed deer annually occurred on only 17% of the study area and preferred more mesic habitats that provided overhead cover adjacent to or interspersed with agricultural fields. Movement patterns of whitetails were not as discrete as those of mule deer and appeared to vary in response to the distribution and availability of forage and cover resources over time. Distribution was even more aggregated than for mule deer and areas of concentration seemed to change through the study. Whitetails also appeared to exhibit relatively high rates of emigration and little home range fidelity. Seasonal home ranges were generally large, but varied among individuals from 0.4 to

8.8 km^2 in summer and from 1.1 to 13.7 km^2 during winter.

Although both species of deer exhibited unique preferences for some individual areas and habitats, neither appeared to have exclusive use of any habitat complex across the study area as a whole. Thus, it seemed that either species could use the entire area in the absence of the other. Direct resource competition apparently was not a factor determining differences in spatial distribution between the two species during this study.

We hypothesized that population regulation occurred through the influence of variable annual precipitation on range forage conditions and herd productivity, which in prairie environments apparently overrides or precludes any influence of population density on reproduction or mortality rates. Despite variable fawn recruitment rates, numbers of adults of both species may stabilize through social interactions that stimulate dispersal of young in the absence of sport hunting or predation.

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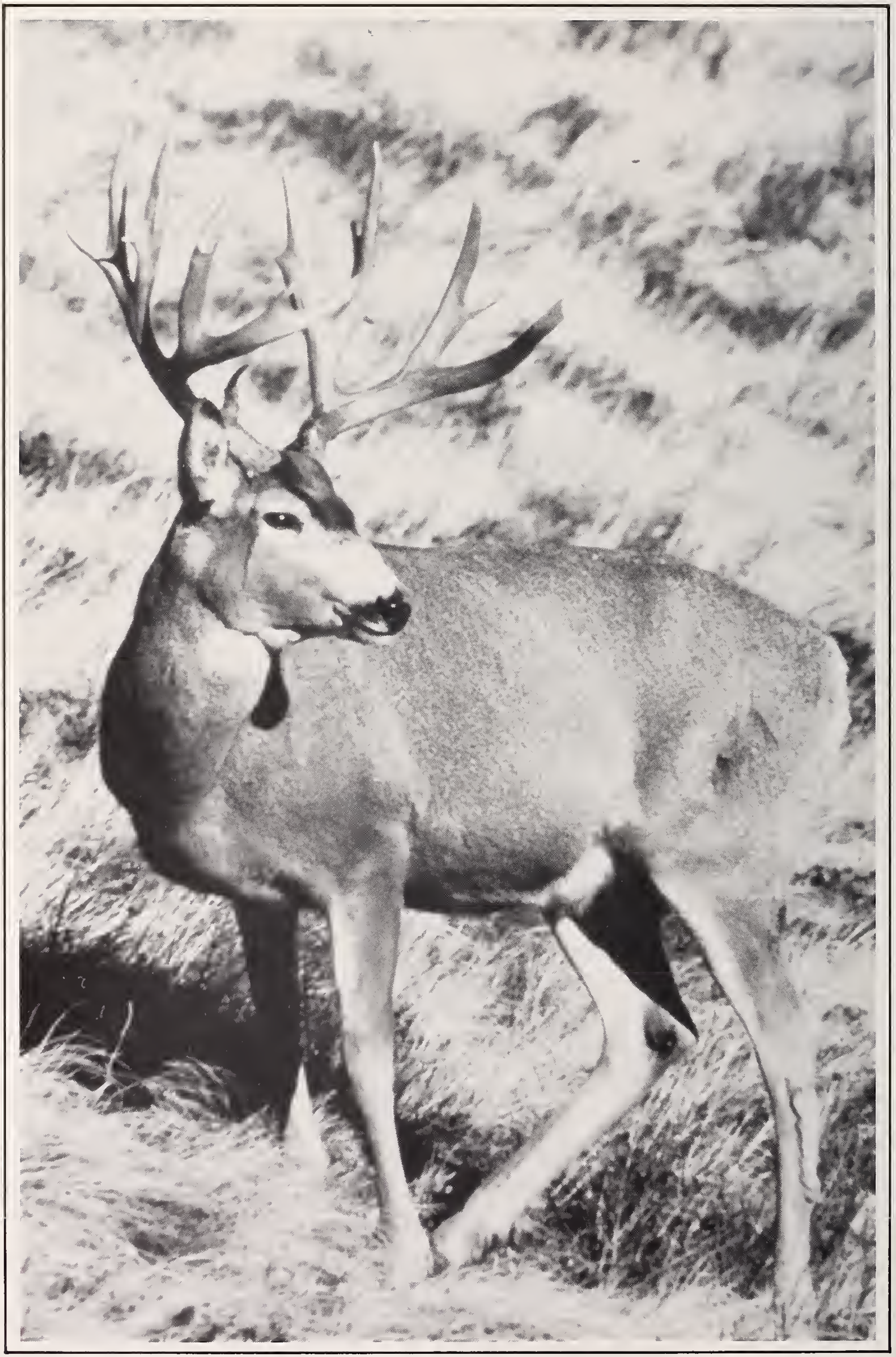


INTRODUCTION

Both Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) and Dakota white-tailed deer *(O. virginianus dakotensis)* occur in the northern Great Plains. Although there is evidence that the two species have different habitat preferences, both can be found in a variety of similar plains habitats.

Aspects of the biology and ecology of both mule deer and whitetails have been studied across a broad spectrum of the habitats in which each occurs, including some plains environments. Past studies on mule deer populations in the region have centered in timbered breaks (Mackie 1970, Hamlin and Mackie 1989) and rough, timbered or brushy uplands (Knapp 1972, Edwards 1977, Dusek 1978, 1980, Phillips et al. 1985). Those in predominantly non-timbered prairie habitats have focused on range relationships between mule deer and cattle (Dusek 1975), movement and habitat use patterns of adults (Severson and Carter 1978), habitat use and mortality rates of fawns (Steigers 1981), effects of hunting on habitat use (Swenson 1982), and winter distribution and habitat use patterns (Swenson et al. 1983).

Research on white-tailed deer in the region has been conducted largely in habitats that include significant coniferous forest (Martinka 1968, Kamps 1969, Kramer 1971, Schneeweis et al. 1972, Dusek 1987), riparian forest (Allen 1968, Compton 1986, Herriges 1986, Dusek et al. 1989), and agricultural (Sparrowe and Springer 1970, Dusek et al. 1988) components. Studies of whitetails occupying primarily rangeland habitats have been limited to evaluations of winter distribution and habitat use in southeastern Montana (Swenson et al. 1983) and the effects of winter weather on reproductive success of deer in the parklands of Alberta (Hall 1973).

Despite these efforts, relatively little is known about population dynamics of either species as related to habitat characteristics in non-timbered prairie environments. Although interspecific relationships between the two species have been studied in several areas where distributions overlap (Martinka 1968, Kamps 1969, Kramer 1973, Anthony and Smith 1977, Wiggers and Beasom 1986), their habitat or niche relationships are not well understood. Many researchers have concluded that different habitat preferences serve to partition the species and minimize opportunity for interspecific competition (Kramer 1973, Wiggers and Beasom 1986); others have identified a potential for direct competition (Anthony and Smith 1977).

Our study began in 1975 as part of a long-term research effort to compare population ecology and habitat relationships of mule deer and white-tailed deer among major habitats in Montana. This effort was initiated because of the inability of existing knowledge to explain widespread declines in deer populations across the state during the early 1970s. Our objectives were to describe and contrast the population ecology, habitat relationships, and factors limiting mule deer and white-tailed deer populations in a representative prairie environment in eastern Montana. Knowledge of species-specific differences in distribution, range use, reproduction, survival, and behavior may provide a better understanding of both population dynamics and regulation in deer populations across the region and the processes that allow the two species to coexist.

STUDY AREA

Location and Environment

The Cherry Creek Study Area (Fig. 1) was located in eastern Montana at 47° north latitude and 106° west longitude, approximately 20 km northwest of Terry, Prairie County, Montana. It encompassed 543 km^2 and extended a maximum of 40 km east to west and 23 km north to south. Land ownership was 55% U.S.D.I. Bureau of Land Management (BLM), 39% private, and 6% State arranged in a checkerboard pattern.

The area was bisected from southwest to northeast by the drainage divide of the Yellowstone and Missouri rivers. The most prominent geographic feature was Big Sheep Mountain, that rises 90 m above the adjacent divide to an elevation of 1,096 m. The terrain sloped gradually on either side of the divide to the lowest point (771 m) in the southeast corner, an elevational change of 325 m over 29 km (Fig. 1). Drainages were relatively narrow near the divide but gradually widened along their length and developed distinct floodplains toward the perimeter of the area.

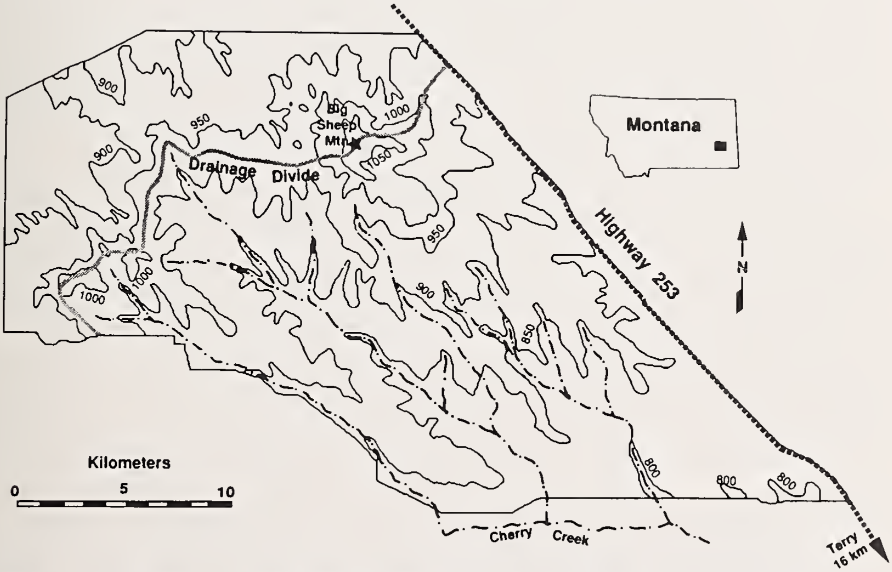


Fig. 1. The Cherry Creek Study Area showing drainage divide, Big Sheep Mountain, and 50m elevation contours.

The climate is semiarid and continental, marked by extreme fluctuations in seasonal and annual temperature and precipitation. Mean annual temperature at the Buffalo Rapids weather station, located approximately 15 km south of the study area, is 6.4 C. Total annual precipitation averaged 28.7 cm, over 70% of which falls from May through September.

The average frost-free season is about 110 days (U.S. Dep. Commerce, N.O.A.A. 1958-1987). However, most growth of native herbaceous plants in the northern plains occurs during April-June (Smoliak 1956), and both plant phenology and production vary widely between years in relation to precipitation and temperatures preceding and during the growing season. Variation in precipitation patterns from year to year is well

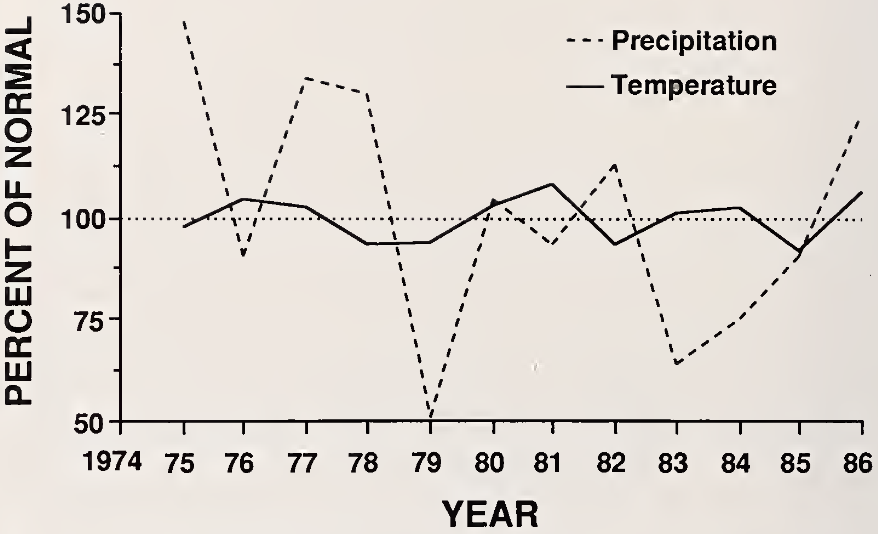


Fig. 2. Annual precipitation and temperature patterns at the Buffalo Rapids weather station, Montana during 1975-1985 recorded as a percentage of the 28-year average.

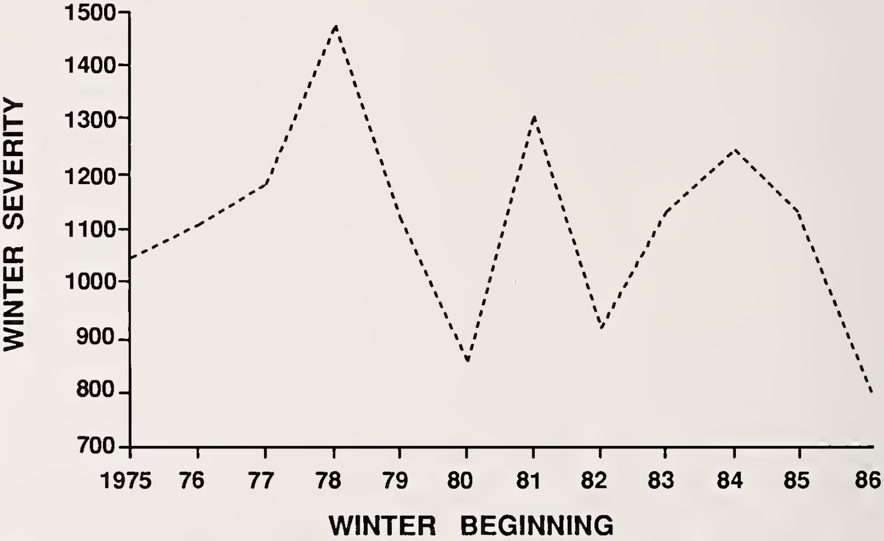


Fig. 3. Winter severity indices for the Cherry Creek study area, 1975-1987.

established as the factor most affecting production of native vegetation in the northern Great Plains (Barker and Whitman 1988). Annual precipitation was below normal during 1976, 1979, 1981, and 1983-1985, when drought conditions prevailed (Fig. 2).

Winter conditions, characterized by subfreezing temperatures and periodic snowfall, generally prevail from November to March. Average snowfall is about 80 cm, but timing and amounts vary annually; significant accumulations are rare. Winter severity varied widely during 1975-1986 (Fig. 3), based on a modified Leckenby Index

(Leckenby and Adams 1986) using daily climatological data from November through March. The most severe winter, 1978-1979, was marked by relatively cold temperatures and complete snow cover from December to March, whereas more mild winters, 1980-1981, 1982-1983 and 1986-1987, were essentially snow-free.

Vegetation

Vegetation of the Cherry Creek area has been generally classified as a wheatgrass-needlegrass type with inclusions of scattered breaks (Barker and Whitman 1988, following Ross and Hunter 1976). For purposes of this study, 8 general habitats were delineated, 6 rangeland and 2 agricultural types. Each represented different vegetation-physiographic units.

Mixed prairie (covering 65% of the area) was characterized by areas of flat to gently rolling topography. Western wheatgrass (*Agropyron smithii*) and needle-and-thread (*Stipa comata*) were the dominant plant species.

Bunchgrass prairie (7% of the area) was dominated by threadleaf sedge (*Carex filifolia*) and bluebunch wheatgrass (*A. spicatum*) and occurred on moderately steep slopes and ridgetops.

Sagebrush grassland (4%) occurred on both upland and floodplain sites. Western wheatgrass and silver sagebrush (*Artemisia cana*) dominated the vegetation. Upland stands were vegetatively similar to the mixed prairies except for an increased shrub component. Floodplain stands were similar to upland stands but also included eastern cottonwoods (*Populus deltoides*) scattered along the drainage channel.

Badlands (18%) were dominated by bluebunch wheatgrass and broom snakeweed (*Gutierrezia sarothrae*). Badlands were characterized more by rough topography and sparsely vegetated, eroding slopes than by any vegetative component. They also contained numerous small inclusions of other native habitats.

Hardwood draws (2%) were identified by the dominance of deciduous trees, particularly green ash (*Fraxinus pennsylvanica*). Vegetative composition met criteria presented by Nelson (1961), indicating a history of moderate grazing pressure. Chokecherry (*Prunus virginiana*) and silver buffaloberry (*Sheperdia argentea*) were commonly found surrounding green ash stands.

Mesic shrubland (1%), dominated by western snowberry (*Symphoricarpos occidentalis*) and Kentucky bluegrass (*Poa pratensis*), occurred in long, narrow bands both above and below the hardwood draws.

Grainfields (3%) averaged about 130 ha with some exceeding 260 ha. Small grain crops consisted primarily of winter wheat with some spring wheat, barley, and oats. They were usually planted on sites that were originally mixed prairies.

Legume hayfields (<1%) included alfalfa or yellow sweetclover fields usually <20 ha, from which a single crop was harvested during July. Hayfields planted on areas that were originally occupied by mixed prairie produced little growth after harvest. Those located in drainages originally dominated by sagebrush grasslands remained green until autumn frosts during most years.

Mixed prairies dominated the landscape, covering large tracts of land. Badlands and bunchgrass prairies covered smaller areas (generally <6 km^2) that were widely scattered throughout the mixed prairies. Badlands and bunchgrass prairies were similar in that both were characterized by hilly terrain that provided more topographic relief than any other habitats. However, the bunchgrass prairies were distinguished from the badlands by their increased vegetative coverage of the surface (primarily with bunchgrasses) and their lack of exposed, eroding soil. Hardwood draws and mesic shrublands were narrow, linear habitats that ran through these other habitats. Sagebrush grasslands were found in both drainages and upland areas of up to 2 km^2.

Mixed prairie, the dominant habitat on the study area. *(Photo by: Richard J. Mackie)*

Mule deer in bunchgrass prairie habitat. *(Photo by: Alan K. Wood)*

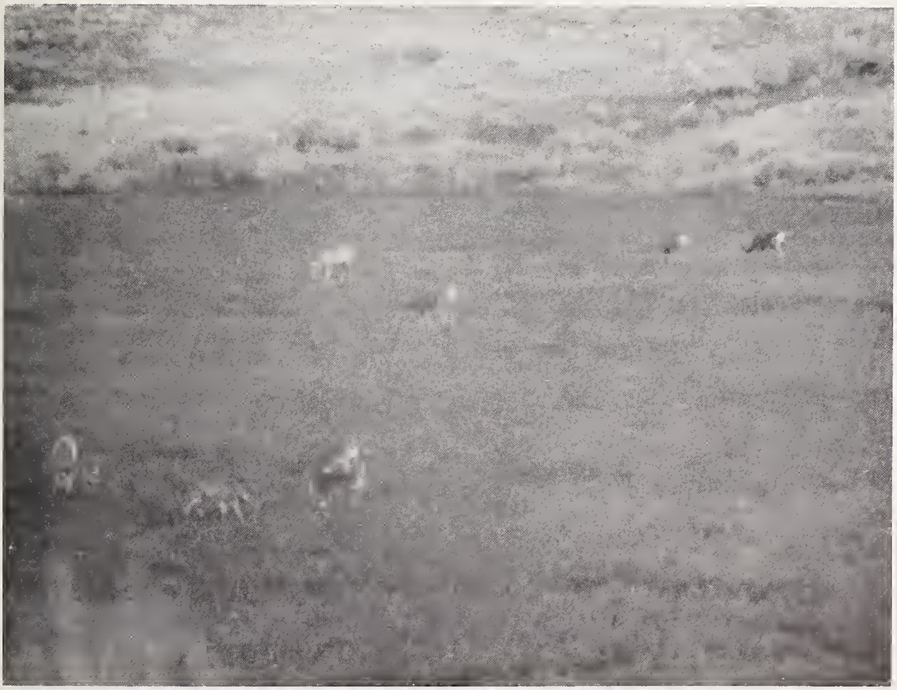
Sagebrush grassland habitat (fore- and mid-ground). *(Photo by: Alan K. Wood)*

Rugged, sparsely vegetated badlands habitat along the Yellowstone-Missouri drainage divide. *(Photo by: Richard J. Mackie)*

Typical hardwood draw habitat in summer. *(Photo by: Alan K. Wood)*

White-tailed deer in mesic shrubland habitat. *(Photo by: Alan K. Wood)*

Grainfield habitat along the northern periphery of the study area. *(Photo by: Alan K. Wood)*



Mule deer (background) and white-tailed deer (foreground) in legume hayfield habitat. *(Photo by: Alan K. Wood)*

Land Use

Livestock grazing has dominated land use on the area since 1890. Although extensive homesteading occurred during 1909-1920, when 1 homestead was established on approximately every 5 km^2, most were abandoned during the 1920s and 1930s. Grazing by cattle predominated during this study. Only 6 of 17 ranches had implemented allotment management plans specifying some type of rest-rotation grazing system, the remaining ranches used the same seasonal pastures each year. According to the U. S. Dep. Agric. Soil Conservation Service (1976), 75% of the rangeland was in good to excellent condition, the remaining 25% was in fair to poor condition. Less than 4% of the area was used for dryland farming.

In most cases private lands were open to the public and provided free access to hunters. Numerous permanent roads and trails allowed vehicle access to within 2.3 km of any point on the area. Many temporary roads were created by hunters driving in search of game, allowing vehicle access to within 720 m of any point on the study area. There were only 3 places where terrain prevented vehicle access to within 500 m and these comprised only 1.5% of the study area.

History of Deer Populations

Mule deer were common in portions of the northern Great Plains during most of the 1800s (Burroughs 1961, Severson 1981). White-tailed deer were locally abundant along major river drainages and tributaries. Populations of both species declined with increasing human presence in eastern Montana from 1872 through 1922, resulting in increasingly restrictive deer hunting seasons. The season was closed in 1923, and only 1 hunting season was allowed from 1923 through 1941. Despite this protection, whitetails had disappeared from much of the region prior to 1941 (Allen 1971). Mule deer numbers remained low through most of that period.

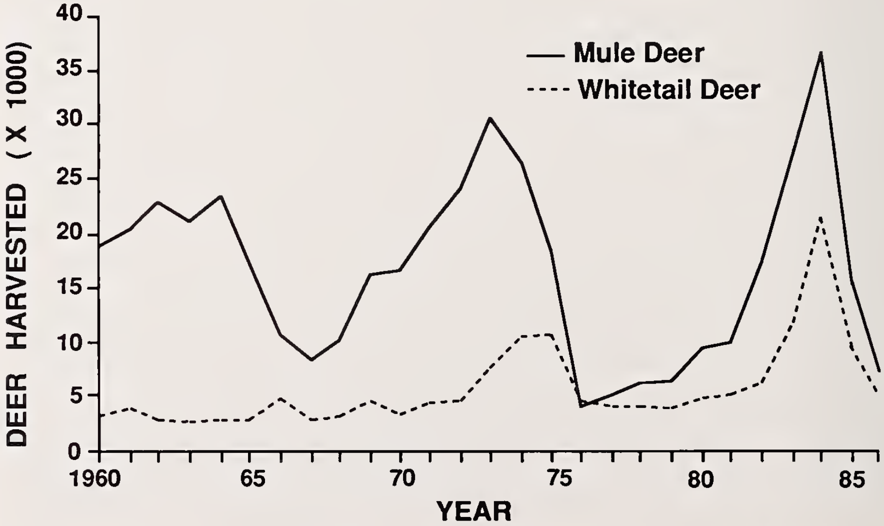


Fig. 4. Mule and white-tailed deer harvest trends in southeastern Montana, reported by the Montana Department of Fish, Wildlife and Parks, 1960-1986.

Expanding populations of both species were evident in eastern Montana during the 1940s and 1950s. The first observations of whitetails on Medicine Lake National Wildlife Refuge in northeastern Montana were made in 1943 (Cook 1945). A report from a long-time resident (L. B. Chapman, pers. commun.) indicated that they first appeared in the Cherry Creek area around 1954. By 1950, mule deer were sufficiently abundant to damage agricultural crops (Egan 1971). Both species have persisted in relative abundance during recent years, though populations have fluctuated widely as indicated by annual harvests from southeastern Montana (Montana Department of Fish, Wildlife and Parks administrative Region 7) (Fig. 4). During 1960-1986, regional mule deer harvests ranged from 4,115 to 36,804, while whitetail harvests varied from 2,622 to 21,292. Densities of both species, but especially mule deer, were relatively low on the Cherry Creek area in 1975-1976 when the study was initiated.

METHODS

Field Methods

Our approach centered around aerial population surveys conducted during September-October, December-January, and March-April of each year, 1975-1980 and 1982-1987. One aerial survey also was conducted during July 1983. All surveys were flown using a Piper SuperCub, at an altitude of 30-60 m, following topographic features to ensure complete coverage of the study area. Morning flights began at daylight and were terminated when activity levels of deer decreased, usually within 2 hours after sunrise. Afternoon flights began as activity levels increased (approximately 2 hours before sunset) and were terminated shortly after sunset.

Deer observed during aerial surveys were classified by species, age, sex, and habitat occupied. When marked deer were available, effort was made to identify each individual observed. Locations were plotted on 1:24,000 topographic maps and later converted to Universal Transverse Mercator coordinates recorded to the nearest 100 m. Individuals were classified as mature males (≥2 years), yearling males (1 year), adult females (≥1 year), and fawns (<1 year) during June-January, as adults or fawns during February-April, and were unclassified during May. All deer were assigned a birthdate of 1 June.

During 1975-1976 and 1982-1987, the entire area also was surveyed from a vehicle during mornings and evenings immediately prior to each aerial survey. Data were recorded as described above except that during autumn and winter surveys, yearling males were classified as spikes (at least 1 unbranched antler) or 2 points (≥2 points/antler). These surveys provided supplementary data on distribution, habitat use, and population characteristics; observations of neck-banded deer during 1983-1987 also were used to document the numbers and identity of marked deer on the study area at the time aerial surveys were flown.

During January and February 1983 and 1984, 151 mule deer (110 females and 41 males) and 34 white-tailed deer (29 females and 5 males) were captured using a drive net (Beasom et al. 1980) or a hand-held net-gun (Barrett et al. 1982). An additional 13 adult mule deer (2 males and 11 females) were captured with the net-gun during February 1986. Deer were manually restrained, ear-tagged, and marked for individual identification. Sixty-nine females (53 mule deer and 16 whitetails) were equipped with radio transmitters (150-151 Mhz). All other deer were fitted with individually recognizable neckbands. Ages were determined by tooth replacement and wear.

Radioed females were located on alternate weeks during 1983 and 1984 using a Piper SuperCub equipped with a directional antenna attached to a wing strut. The timing of locations varied among seasons. During summer (Jun-Sep), 60% of all locations were made 0-3 hours after sunrise. During autumn (Oct-Nov), 50% were made 2-4 hours after sunrise. During winter (Dec-Mar), 56% were made between 1100-1300 hours. All other locations, including those during spring (Apr-May), were made throughout the remaining daylight hours. Locations and other data were recorded as during aerial surveys.

Spotlight counts of deer in 5 alfalfa fields were conducted weekly during July-October, 1983 and 1984, to evaluate nocturnal habitat use patterns in and around these fields. Counts were made approximately 1.5 hours after sunset using a 300,000 candle power white light. Numbers of deer of both species and identification and location of any marked deer were recorded. Locations of all marked deer observed during radio-location flights, aerial surveys, and ground-based observations were combined for home range calculations yielding an average of 1 observation every 8 days.

Analytical Methods

Population Estimates and Analyses

Population estimates were derived from aerial survey data following concepts of Mackie et al. (1981). Survey efficiency (proportion of total deer present that was observed) was increased by relatively sparse tree and shrub cover on the area. Efficiency was generally high, ranging from 51 to 87% for mule deer and 31 to 67% among whitetails (Table 1) as reported for aerial surveys in other relatively open habitats in Montana (Mackie et al. 1981, Hamlin, unpubl. data). Efficiency also was increased by conducting surveys during early morning and evening hours when deer

Table 1. Estimated efficiencies of aerial surveys as measured by the percent of marked deer seen during aerial surveys on the Cherry Creek study area during autumn, winter, and spring, 1983-1987.

Season	Pilot	Mule deer	Whitetails
Autumn			
Oct. 1983	T	51	53
Oct. 1984	S	57	47
Sep. 1985	C	54	31
Oct. 1986	W	52	
Mean ± SE		53.5±1.3	43.7±6.6
Winter			
Dec. 1983	T	65	54
Dec. 1984	K	68	50
Dec. 1985	C	86	50
Dec. 1986	K	62	
Mean ± SE		70.3±5.4	51.3±1.3
Spring			
Mar. 1983	T	65	39
Apr. 1984	K	58	67
Mar. 1985	S	58	57
Apr. 1986	K	59	65
Apr. 1987	W	87	
Mean ± SE		65.4±5.6	57.0±6.4

were most active and tended to move out of any concealing cover. Use of complete-coverage surveys eliminated possible biases resulting from sampling schemes such as quadrat or transect surveys that require precise designs to ensure adequate population sampling. In addition, counts obtained from complete coverage surveys represent absolute minimum population estimates.

Preliminary population estimates during 1983-1987 were derived using the Lincoln index (Davis and Winstead 1980). An average of 9% (range 4-13%) of all deer on the area was marked. Final population estimates for each season and year were calculated using arithmetic modeling to reconcile initial estimates with known or estimated mortality and natality based on herd classifications, hunting statistics, survival rates of marked deer, and population estimates and herd composition from prior and subsequent seasonal estimates. This approach tended to smooth population estimates and helped to avoid many of the problems associated with use of a single estimate (McCullough and Hirth 1988). Estimated mule deer numbers for autumn 1982 were calculated from the January 1983 estimate using change-in-ratio procedures (Davis and Winstead 1980). July estimates were based on spring population estimates, mortality rates of marked deer from April to July, pregnancy rates (Wood 1987), and average litter size of females with fawns during July.

Seasonal and annual population estimates from winter 1975-1976 through spring 1982 were developed primarily to indicate population trends; none was used directly in statistical analyses. Estimates for winter 1975 and spring 1976 were derived by summing maximum counts made in localized areas during a series of aerial and ground-based surveys that winter. Population trends for 1977-1980 were based on aerial surveys during winter and spring each year. Initial population estimates were generated by assuming that 85% of the population was observed. This correction was based on 1975-1976 estimates, visibility of deer in 3 other areas of eastern Montana (K. L. Hamlin, unpubl. data), and survey efficiency on the study area during 1983-1987 (Table 1). Final estimates were calculated using arithmetic modeling to reconcile total numbers and sex and age composition between successive seasons with observed ratios, estimated mortality rates, and/or any additional population data available. Mule deer population estimates for April 1981 and 1982 were extrapolated from spring estimates of 1980 and autumn estimates of 1982, respectively.

Population estimates for whitetails probably were less precise than those for mule deer, especially during 1975-1982. Possible reasons include smaller numbers of marked deer, more variable survey efficiencies, more extensive movement, more variable distribution, and smaller samples in seasonal counts and classifications. As noted above, estimates for those years were used primarily to define population trends of both species.

Seasonal and annual exponential mortality rates (r) from 1982 to 1987 were estimated directly from population estimates using the formula:

$$r=\ln(N_{t+1}/N_t)$$

where

N_{t+1} = number at time t+1 and

N_t is the number at time t.

Exponential mortality rates were converted to finite rates of change (F) by the formula:

$$F = e^r - 1$$

(Caughley 1977:51-52).

The influence of seasonal precipitation patterns on fawn survival was evaluated by correlating total precipitation received from July through April prior to fawning season with estimates of percent fawns the following winter and spring. Relationships between winter severity and population characteristics and trend were evaluated using calculated winter severity indices (Fig. 3).

Habitat Use and Relationships

Distribution, movements, home range areas, and habitat relationships were analyzed on the basis of data obtained from aerial surveys, relocations of radio-collared and neck-banded deer, and vehicle and spotlight surveys during 1982-1986. Data obtained during surveys from 1975 through 1980 provided general comparative or supplementary information.

Seasonal and study-long estimates of average activity radii (AARs) (Hayne 1949) and convex polygon areas (Mohr 1947) were calculated using the TELDAY computer program (T. N. Lonner and D. E. Burkhalter, Users manual for the computer program TELDAY, Mont. Dep. of Fish, Wildl., and Parks, unpubl. 15 pp.). AARs were used as an index of home range size or mobility in statistical analyses because they are less sensitive to outlying locations than convex polygons (MacDonald et al. 1980). Also, data derived from these estimates more nearly approximate a normal distribution because of the central limit theorem and therefore can be more readily analyzed using parametric statistics. Determination of which months to include in each season was based on major changes in movements and habitat use.

Monthly AARs were calculated using 2-5 points/animal/month (Dusek and Wood 1986), based on relocations of radio-collared female mule deer, neck-banded male mule deer, and all marked female white-tailed deer. Observations of neck-banded female mule deer were not used because an analysis of variance (ANOVA) indicated significant differences in average monthly AARs due to the interaction of band type (neckband or radio) and month.

Habitat selection was analyzed on the basis of data obtained during all aerial surveys from 1975 through 1985 and relocation of radio-collared females during 1983-1985. The survey data may have been most indicative of overall selection patterns because they were collected throughout the study and avoided possible biases caused by an unrepresentative distribution of radioed deer. However, data from radio-collared females were less likely to be affected by potential visibility biases in some habitats. Tests for selection (use > availability) or avoidance (use < availability) of each of 8 habitats on the area were conducted using Chi-square goodness-of-fit procedures and 95% Bonferroni confidence intervals (Byers et al. 1984). Habitat availability was determined from maps drawn on orthophotoquads using infrared aerial photographs (Wood 1987). Habitat availability for analysis of survey data was based on the amount of each habitat mapped within survey area boundaries. Availability relative to electronically determined locations of radioed females was measured over a larger area determined by deer movements.

Evaluations of habitat selection or avoidance only determined the extent to which various habitats were used. To determine the effects of habitat characteristics (type, amount, and interspersion) on deer distribution, movements, and home range size, the study area was divided into 2,172 25-ha grid cells (Porter and Church 1987). The amount of area occupied by each habitat, meters of edge/ha of each habitat, and a

Shannon-Weaver diversity index (Shannon and Weaver 1949) were calculated in each 25-ha cell. Comparisons were made on the basis of migration class (3), season (2), home range size (5 largest vs. 5 smallest), and contrasting intensities of use (high use ≥ 3 observations/cell, low use = 1 observation/cell). This analysis should identify habitat characteristics or complexes that influenced deer distribution, mobility, and density because only occupied cells were used. We assumed that smaller home ranges and cells used intensively were located in areas with a higher quantity and/or quality of resources.

Interspecific overlap in distribution (using aerial survey locations) and habitat use (using radio-location data) was evaluated by calculating niche overlap indices (Hurlbert 1978). The niche overlap index L, has a value of 0 when no resources are shared, 1 when both species use resources in proportion to availability, and is >1 when use exceeds availability and preferences tend to coincide. A directional index of interspecific crowding $Z_{x(y)}$, quantifies "the density of species y encountered, on the average, by an individual of species x" (Hurlbert 1978:71). These indices incorporate the effects of both resource availability and relative density on interspecific overlap. L values are comparable between seasons but Z values are not because they incorporate direct measures of population density (Hurlbert 1978) that were biased by differences in seasonal visibility of deer. Habitat characteristics in areas of interspecific overlap and exclusive use were calculated using 25-ha cells occupied by deer observed during aerial surveys.

Statistical Analyses

Different statistical procedures were selected based on the hypotheses tested and how well data met assumptions of each test. Comparisons of summer and winter AARs used paired-sample *t* tests to control for variation in home range size between deer. One-way or factorial ANOVAs were used when the assumptions of normally distributed data and equality of variances among groups were met. Multiple mean comparisons were then conducted using least significant difference (LSD) tests. Those data failing tests of variance equality were analyzed using ANOVA on ranks of the data (Conover and Iman 1981) with multiple comparisons using LSD tests on ranks. Data not normally distributed were analyzed using Kruskal-Wallis Chi-square approximations with multiple comparisons via Wilcoxon rank sum tests.

One exception was the analysis of habitat complexes in 25-ha cells. We chose to reduce the number of habitat variables analyzed by using discriminant analysis to identify variables most likely to differentiate between groups because up to 816 tests would be required (2 species x 2 seasons x 17 habitat variables x 2-3 groups x 4 data sets) on the original data. However, tests for statistical significance were done using Wilcoxon tests on the variables identified by discriminant analysis because these data exhibited a highly skewed distribution.

Categorical data were analyzed using Chi-square contingency tests of independence or goodness-of-fit as appropriate. Correlation analyses were done using the least squares technique (to calculate r values and probabilities of non-zero slopes) unless data were not normally distributed or only qualitative associations were evaluated, in which case Spearman rank correlation procedures (r_s) were used. All statistical analyses were completed using the Statistical Analysis System (SAS Inst. Inc. 1985).

POPULATION CHARACTERISTICS AND DYNAMICS

Mule Deer

Population Trends

Approximately 180 mule deer occurred on the study area in spring 1976. Estimated spring populations increased consistently to a peak of about 1,080 in 1983 and 1984. Thereafter, numbers declined annually to approximately 347 in spring 1987 (Fig. 5, Table 2). Other seasonal population estimates followed similar trends, although summer and autumn populations peaked in 1983 and declined steadily through the remainder of the study. Population size reached a maximum of 1,818 deer in July 1983, a 10-fold increase in 7 years. During the principal period of population growth, from 1976 to 1982, the finite rate of increase averaged 29% per year (SE = 0.92%).

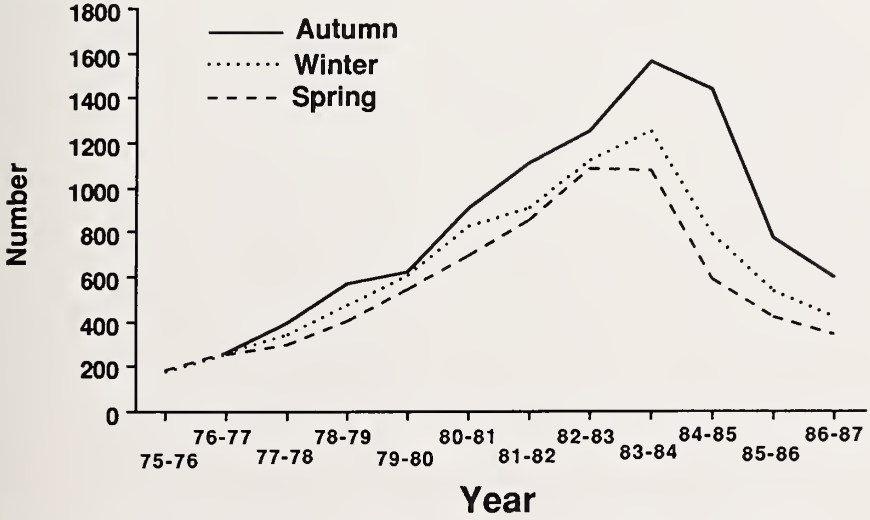


Fig. 5. **Estimated mule deer population trends on the Cherry Creek study area for autumn, early winter and early spring, 1975-1987.**

Actual counts generally showed the same trends as population estimates, except for winter and spring 1980 when surveys were less complete or intensive. Both counts and estimates documented the extreme low in 1976, the peak in 1983-1984, and subsequent decline. They also were consistent with trends indicated by data from other mule deer research and management trend areas in central and eastern Montana, though the timing and rates of increase and decline may have varied somewhat (Mackie et al. 1985). Reviews of statewide data indicated that mule deer populations were generally low throughout Montana during 1976 as a result of declines during the early-mid 1970s. Increasing populations were evident locally by 1978 and generally across the state by 1979-1980. Peaks occurred in most areas during 1982-1984.

Table 2. Estimated mule deer population size and sex and age composition on the Cherry Creek area at the beginning of each season, 1982-1987.

Date	Total	Adults	Fawns	Females	Males	
					Mature	Yearling
Summer 1982	1,538	858	680	655	77	126
Autumn 1982	1,252	841	411	642	77	122
Winter 1982	1,121	710	411	634	31	45
Spring 1983	1,083	710	373	634	31	45
Summer 1983	1,818	1,083	735	744	151	188
Autumn 1983	1,558	1,064	494	735	151	178
Winter 1983	1,257	806	451	672	41	93
Spring 1984	1,074	776	298	647	39	90
Summer 1984	1,722	1,074	648	768	129	177
Autumn 1984	1,441	1,031	410	747	129	155
Winter 1984	795	571	224	472	38	61
Spring 1985	595	536	59	443	36	57
Summer 1985	996	595	401	467	107	21
Autumn 1985	775	590	185	465	107	18
Winter 1985	538	405	133	340	56	9
Spring 1986	421	360	61	298	53	9
Summer 1986	833	413	420	332	62	19
Autumn 1986	603	413	190	332	62	19
Winter 1986	420	263	157	229	23	11
Spring 1987	347	255	92	222	22	11

Declines that began in spring 1984 in some areas continued through 1985-1986. Overall trends in mule deer numbers on an intensively studied area in the Missouri River Breaks, approximately 225 km northwest of Cherry Creek, generally paralleled those on the Cherry Creek area from 1976 through 1985 (Hamlin and Mackie 1989). Subsequently, the Breaks population recovered and increased during 1986, whereas that on Cherry Creek continued to decline.

Productivity and Herd Composition

Initial fawn production was not measured directly. Limited data on pregnancy rates and litter size among marked females observed during summers 1983-1985 (Wood 1987) and fawn:doe ratios recorded in autumn, winter, and spring surveys throughout the study indicated that productivity was generally high. Pregnancy rates (56, 97, and 88% for females age 1.5, 2.5-7.5, and ≥8.5 years, respectively) were measured only during years when productivity may have been depressed by drought and poor range conditions, but were similar to those reported for mule deer in other habitats (Anderson 1981, Beasom and Wiggers 1984).

Litter size for females with fawns averaged 1.50, 1.43, 1.29, 1.27, and 1.54 during

Table 3. Mule deer buck:doe:fawn ratios during autumn, winter, and spring on the Cherry Creek area, 1975-1987, estimated from aerial surveys (sample size in parenthesis) and/or as indicated.

	Autumn	Winter	Spring
Year	buck:doe:fawn	buck:doe:fawn	buck:doe:fawn[a]
1975-1976	30:100:48[b]	7:100:48 (101)	7:100:48 (116)
1976-1977	42:100:67 (119)	36:100:66 (213)	36:100:66 (155)
1977-1978	51:100:79 (213)	31:100:74 (348)	30:100:56 (294)
1978-1979	45:100:111[b,c]	19:100:111 (435)	19:100:90 (298)
1979-1980	17:100:102[b]	10:100:102 (293)	11:100:82 (174)
1980-1981	36:100:90[d]	18:100:90[e]	18:100:78[d]
1981-1982	28:100:90[d]	12:100:85[e]	12:100:75[d]
1982-1983	31:100:66 (473)	12:100:66 (542)	12:100:59 (700)
1983-1984	45:100:67 (795)	20:100:67 (685)	20:100:46 (637)
1984-1985	38:100:55 (752)	21:100:47 (541)	21:100:13 (347)
1985-1986	27:100:40 (419)	19:100:39 (462)	18:100:20 (386)
1986-1987	33:100:65 (314)	15:100:70 (261)	16:100:41 (301)
Mean	35:100:73	18:100:72	18:100:56

[a] Doe:fawn estimate based on fawn:adult ratio during spring survey and estimated male:female ratio from preceeding early winter survey or population estimate.

[b] Minimum estimate based on fawn:female and fawn:adult ratios during subsequent early winter and spring surveys.

[c] Estimate derived using fawn:adult ratio from aerial survey in winter and male:female ratio from population estimate.

[d] Estimate derived from aerial classification by regional wildlife management biologist on and adjacent to study area.

[e] Estimate based on interpolation between fawn:female and fawn:adult ratios observed in classifications on and adjacent to the study area during aerial surveys in autumn and spring.

Table 4. Seasonal mortality rates (%) for mule deer on the Cherry Creek study area, 1982-1987.

Year	Season	Total adult	Fawn	Adult female	Adult male
1982-1983	Annual	17	46	3	63
	Spring/summer	2	40[a]	2	2
	Autumn	16	0	1	62
	Winter	0	11	0	0
1983-1984	Annual	28	59	13	62
	Spring/summer	2	33	1	3
	Autumn	24	9	9	59
	Winter	4	34	4	4
1984-1985	Annual	50	91	42	70
	Spring/summer	4	37	3	7
	Autumn	45	45	37	65
	Winter	6	74	6	6
1985-1986	Annual	40	85	36	52
	Spring/summer	1	54	0	2
	Autumn	32	28	27	48
	Winter	11	54	12	5
1986-1987	Annual	38	78	33	59
	Spring/summer	0	55	0	0
	Autumn	36	17	31	58
	Winter	3	41	3	3
Mean	Annual	35	72	25	61
	Spring/summer	2	44	1	3
	Autumn	31	20	21	58
	Winter	5	43	5	4

[a] Rates for fawns are calculated for summer only.

July from 1982 to 1986, respectively, and followed the same general trend as fawn:doe ratios. Over all years, fawn:doe ratios averaged 73:100 in autumn, 72:100 in winter and 56:100 in spring (Table 3). Both litter size and fawn:doe ratios were low during 1984 and 1985 following 2 and 3 consecutive years of drought. These data indicated that fawn survival also remained relatively high throughout most of the study.

Generally, fawn recruitment based on ratios in spring was above average to high during years of increasing to peak populations (1977-1982). Recruitment was near average in 1983, but decreased sharply to lows in 1985 and 1986 as the population declined. Although recruitment increased in spring 1987, it remained below average in association with a further decline in mule deer numbers on the area. The trends in fawn production and recruitment on the study area during 1976-1986 generally mirrored those for mule deer in other areas of central and eastern Montana during the period as indicated by other research and management surveys.

The proportion of yearling males in the population (Table 2) indicated that fawns surviving until spring were being recruited into the adult population. Yearling males comprised an average of 11 % (range 3-17%) of the population during 1982-1986, but relatively few occurred during 1985 and 1986 following years of low fawn:doe ratios in spring. Overall male:female ratios were relatively high during autumn (35:100) (range 17-51) (Table 3). Male:female ratios dropped following hunting season.

Mortality Patterns and Rates

Seasonal, annual, and mean seasonal and annual mortality rates were calculated only during 1982-1983 through 1986-1987 when data were most complete and population size and composition were determined for summer, early autumn, early winter, and spring (Table 4). Summer and total mortality rates for fawns do not include deaths at parturition or during the early post-natal period in June. In addition, all rates reflect conditions that prevailed during 1982-1987, when populations peaked and declined as a result of low fawn survival and increased adult mortality. Thus, the seasonal and annual means may be somewhat higher than actually prevailed through the entire study. As noted earlier, increasing populations during 1977-1982 were characterized by above-average fawn recruitment. They were likely associated with reduced adult mortality as well, especially from hunting.

Fawn mortality rates based on numbers in the population at the beginning of each season were relatively high during summer ($\overline{X} = 44\%$), declined in autumn ($\overline{X} = 20\%$), and increased again over winter ($\overline{X} = 43\%$). On a monthly basis, however, average mortality rates decreased as fawns matured, dropping from 18%/month during July-September to 12%/month during October-April.

Natural mortality rates of fawns during autumn were higher than fawn harvest rates. Fawns comprised only 8% of 205 harvested mule deer examined from 1982 to 1984 when they made up 32-38% of autumn populations. Based on fawn:doe ratios of deer shot during hunting season, estimated total harvests, and numbers of fawns in populations following the hunting season, natural mortality rates of fawns during autumn averaged 0, 8, 23, and 21% during 1982-1985, respectively; corresponding harvest rates averaged 0, 1, 22, and 7%, respectively.

Annual mortality rates of adult females averaged 25% (Table 4). Mortality rates were highest during autumn, averaging 21% from 1982 to 1986. They averaged only 6% through all other seasons.

Table 5. Number of marked mule deer lost from the Cherry Creek population by season, 1983-1987.

Sex	Age	No. alive	Season	Cause Hunting	Natural	Total
F	0	28	Winter	0	4	4
M	0	26	Winter	0	2	2
F	≥1	117	Summer	0	5[a]	5
			Autumn	57	0	57
			Winter	0	7	7
M	≥1	41	Summer	0	16[b]	16
			Autumn	17	0	17
			Winter	0	0	0
	Total	212	All	74	34	108

[a] One female dispersed from the study area.

[b] All 16 males dispersed from the study area.

Hunting was the leading cause of death among marked adult females through the year and the sole cause of mortality during autumn (Table 5). Eighty-three percent of all marked adult females that died were shot. Crippling losses and illegal kills, which comprised 10 (16%) of the 57 marked females that died during the hunting season, were included in the total harvest and calculated harvest mortality rates.

The remaining 17% of the annual deaths of marked adult females resulted from a variety of other causes, none of which contributed significantly to overall mortality rates. Two deaths resulted from deer getting a front foot entangled in their collars. During winter, 3 cases of malnutrition and 1 coyote (*Canis latrans*) kill were confirmed. Another marked female died from undetermined causes. During summer, 1 marked female left the area, 1 was killed by coyotes, 2 died from collisions with vehicles, and 1 disappeared.

Annual mortality rates of adult males averaged 61%. Mortality rates averaged 58% during autumn and only 5% throughout the remainder of the year (Table 4). Hunting was the only cause of death identified among marked adult males (Table 5). Twelve marked males were shot and reported by hunters; 5 others disappeared during hunting season and were presumed shot. No crippling loss or illegal kill was documented among marked males, although 12 unmarked males were found dead of those causes. Only 7 unmarked males were found that had died from causes other than hunting.

Immigration and Emigration

In terms of population dynamics, immigration and emigration represent gains and losses, or special cases of "recruitment" and "mortality", respectively, and must be considered in relation to those parameters. The Cherry Creek study area comprised an open population-habitat unit surrounded by similar patchy or variable habitat from or to which deer could move. Because deer were marked only on the study area, we could not detect or measure immigration directly. Nonetheless, some indication of emigration patterns and rates was obtained from observations and other records of marked individuals during 1983-1986.

Overall, only 7 instances of emigration were confirmed among the 110 female and 67 male mule deer marked. Another 13 marked male fawns were classified as emigrants because they were consistently observed on the area from January through June and began to disappear during summer when yearling emigration normally begins (Bunnell and Harestad 1983). We assumed that no fawns emigrated prior to marking at approximately 8 months of age, as indicated by other studies (Robinette 1966, Bunnell and Harestad 1983).

Among females, only 1 of 29 yearlings, 1 of 32 2-year-olds, and 1 of 49 3-years and older left the area. Thus, emigration did not appear to contribute significantly to net "mortality" of females on the area. This also was indicated by consistency in estimates of adult female numbers in summer and autumn populations during 1983-1986. Any emigration that did occur was probably balanced by immigration.

In contrast, relatively high rates of emigration were evident for young males. Sixteen (67%) of 24 yearlings and 1 (5%) of 20 2-year olds emigrated. No marked male 3-years and older left the area. Slight declines in numbers of yearling males between estimated summer and autumn populations indicated that a net loss of males attributable to emigration may have occurred during all years except 1986. However, because summer mortality rates for yearling males were low (3-14% during 1982-1986), most emigration during summer must have been compensated by immigration of yearling males from adjoining habitats. A similar pattern of high emigration rates by yearling males balanced by immigration was observed during long-term studies of mule deer in the Missouri River Breaks (Hamlin and Mackie 1989).

White-tailed Deer

Population Trends

Approximately 200 whitetails occurred on the area during winter and spring 1975-1976. Numbers in autumn and early winter populations appeared to remain relatively stable until 1978, while those in spring declined by about one-third. Thereafter, all seasonal estimates indicated annual increases through 1982-1983, when approximately 429, 351, and 335 occurred during autumn, winter, and spring, respectively (Fig. 6, Table 6). The peak in spring numbers during 1983 carried over to an apparent overall peak population of approximately 585 in summer 1983, when data were first available to estimate summer population size.

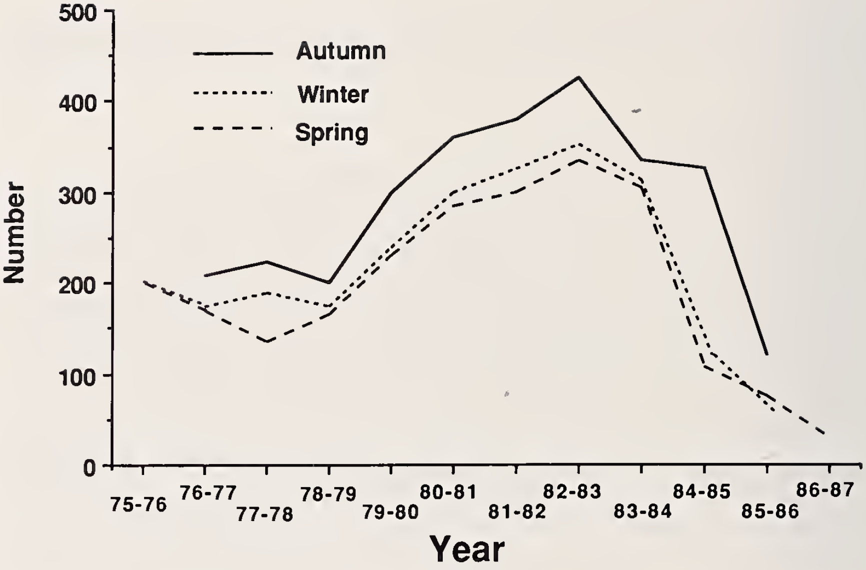


Fig. 6. Estimated white-tailed deer population trends on the Cherry Creek study area for autumn, early winter and early spring, 1975-1987.

Declining whitetail numbers were first evident in estimates for autumn, winter, and spring 1983-1984. Sharp declines occurred during 1984-1986 (Fig. 6, Table 6). Only 16 whitetails were counted on the area during the aerial surveys in early winter 1986 and 9 in spring 1987, when a maximum residual population of 30 was estimated.

Overall, during 1975-1986, estimates indicated seasonal populations approximately doubled from 1978 through 1982, then decreased by 70-80% by 1985-1986. The difference between the estimated high summer population of 585 in summer 1983 and the low of 30 in spring 1987 represented a nearly 20-fold fluctuation in total numbers during this study.

Whitetail population trends on the Cherry Creek area during 1975-1986 generally followed those indicated for white-tailed deer by other research and management studies in eastern Montana. Populations were relatively low or varied among habitats during the mid 1970s, increased to peaks and perhaps all time highs during 1982-1983, and stabilized or declined during 1983-1985 (Mackie et al. 1985). Data for white-tailed deer populations along the lower Yellowstone River (Dusek et al. 1989) indicated trends very similar to those observed on our study area, though the magnitude of decline from 1983 through 1986 was much less on that area.

Productivity and Herd Composition

Data on initial productivity of whitetails were limited to a small sample tested for pregnancy during 1983-1985, fawn:doe ratios derived from observations of marked females during summer 1983 and 1984, and classifications during all aerial surveys in autumn and winter. Pregnancy tests showed all but one (a 2-year-old) of 12 females examined were pregnant (Wood 1987).

Although fawn:female ratios derived from seasonal aerial classifications (Table 7) may not be precise for some seasons and years because of small sample sizes,

Table 6. Estimated white-tailed deer population size and sex and age composition on the Cherry Creek area at the beginning of each season, 1982-1987.

Date	Total	Adults	Fawns	Females	Males
Autumn 1982	429	256	173	186	70
Winter 1982	351	239	112	181	58
Spring 1983	335	230	105	174	56
Summer 1983	585	315	270	210	105
Autumn 1983	335	252	83	176	76
Winter 1983	312	235	77	160	75
Spring 1984	303	233	70	159	74
Summer 1984	484	303	181	194	109
Autumn 1984	326	232	94	174	58
Winter 1984	120	96	24	70	26
Spring 1985	107	91	16	66	25
Summer 1985	175	107	68	74	33
Autumn 1985	120	105	15	73	32
Winter 1985	64	51	13	35	16
Spring 1986	75	60	15	41	19
Spring 1987	30	20	10		

possible biases in observability, and movements off the survey area, they indicate that productivity was generally high. On average, there were approximately 77 fawns:100 females in the population in autumn, 74:100 in early winter, and 66:100 in spring. The moderate or minor decrease in fawn:female ratios from autumn to spring during most years indicated that fawn survival and recruitment also were relatively high.

Fawn recruitment was above average during most seasons and years from 1975-1976 through autumn 1982, except for spring 1978. Below average recruitment was indicated by fawn:female ratios for all seasons and years from winter 1982 through spring 1986. Fawns comprised 50% of the small number of white-tailed deer observed in spring 1987, suggesting a possible increase in recruitment as observed for mule deer.

Table 7. White-tailed deer buck:doe:fawn ratios during autumn, winter, and spring on the Cherry Creek area, 1975-1987, estimated from aerial surveys (sample size in parenthesis) and/or as indicated.

	Autumn	Winter	Spring
Year	buck:doe:fawn	buck:doe:fawn	buck:doe:fawn[a]
1975-1976	40:100:80 (27)	25:100:75 (170)	25:100:75 (172)
1976-1977	40:100:73[b]	22:100:73 (128)	22:100:73 (53)
1977-1978	36:100:68 (83)	20:100:70 (160)[a]	22:100:28 (116)
1978-1979	35:100:75[c]	17:100:78 (100)[a]	17:100:67 (59)
1979-1980	38:100:117[b]	20:100:117 (165)	20:100:110 (98)
1980-1981	36:100:121[d]	20:100:120[e]	20:100:108[d]
1981-1982	33:100:95[d]	20:100:95[e]	20:100:95[d]
1982-1983	35:100:93 (148)	32:100:62 (169)	32:100:60 (133)
1983-1984	43:100:47 (185)	47:100:48 (127)	47:100:44 (203)
1984-1985	33:100:54 (152)	37:100:34 (60)	38:100:24 (61)
1985-1986	44:100:21 (37)	46:100:37 (32)	46:100:37 (59)
Mean	38:100:77	28:100:74	28:100:66

[a] Doe:fawn ratios based on fawn:adult ratio during spring survey and estimated male:female ratio from preceeding early winter survey or population estimate.

[b] Minimum estimate based on fawn:female and fawn:adult ratios during subsequent early winter and spring surveys.

[c] Estimate derived from fawn:adult ratio from aerial survey in winter and male:female ratio from population estimate.

[d] Estimate derived from aerial classification by regional wildlife management biologist on and adjacent to study area.

[e] Estimate based on interpolation between fawn:female and fawn:adult ratios observed in classifications on and adjacent to the study area during aerial surveys in autumn and spring.

Differences between sex ratios for autumn and early winter during 1975-1980 and between winter sex ratios during those years and 1982-1986 (Table 7) were probably related to the time surveys were conducted. Antler drop in white-tailed deer on the area begins in mid-December and progresses rapidly through January. The 1975-1980 early winter surveys were all completed in late December or January, when some males without antlers may have been misclassified as females from the air. All of the surveys during 1982-1986 were completed in early-mid December, before antler drop.

Differences in ratios among years also were influenced by differential harvests of adult males and females as determined by numbers of antlerless permits issued. Other factors, such as the number or proportion of spike-antlered yearling males, annual differences in time or rate of emigration, and the extensive movements of most white-tailed deer on the area, also may have influenced seasonal and annual variations in sex ratios observed during the study.

Mortality Patterns and Rates

Mortality rates for white-tailed deer were calculated only for the period 1982-1983 through 1985-1986, when data were most complete and population size and composition were estimated with greater precision than earlier years. Consequently, these data largely reflect patterns and rates more characteristic of a period when fawn survival was low and the population was declining rather than average patterns and rates that may have prevailed over the entire period of study.

Average fawn mortality rates for whitetails were high during summer ($\overline{X} = 65\%$), moderate during autumn ($\overline{X} = 32\%$), and relatively low during winter ($\overline{X} = 12\%$) (Table 8). Monthly mortality rates averaged 30%/month during July-September, 18%/month October-November, and 3%/month December-April. A very similar pattern of fawn mortality was reported for white-tailed deer along bottomlands of the lower Yellowstone River during 1980-1986 (Dusek et al. 1989). Because fewer whitetails were marked and examined in field checks of hunters, we were not able to partition autumn mortality between natural and harvest rates as for mule deer.

Numbers of adult males and females declined from spring through summer during 1983-1985, when an average of about 9% of the females and 26% of the males were lost from the population (Table 8). The late spring/summer mortality rate among females was highest during 1983, at peak population densities, and decreased as the population declined. Records of marked deer (Table 9) suggested that this decline resulted largely from dispersal, although some natural mortality was documented. The only marked adult male whitetail on the area during summer 1984 died of epizootic hemorrhagic disease (EHD) during September. EHD also was the suspected cause of death for 5 unmarked deer found dead during the October 1984 aerial survey. Overall, only 1 of 25 marked deer died, indicating that the effect of EHD on the population was probably minimal.

As noted earlier, population data were not sufficiently precise to calculate and evaluate mortality rates during years prior to 1983. However, the fact that autumn and early winter populations remained relative stable during 1975-1978 and increased modestly during 1979-1982 despite average to high fawn recruitment in most years suggested that some summer mortality or emigration of adults probably occurred throughout the study.

Most mortality among adult females during 1982-1985 occurred in autumn when

Table 8. Seasonal mortality rates (%) for white-tailed deer on the Cherry Creek area during 1982-1986.

Year	Season	Total adult	Fawn	Adult female	Adult male
1982-1983	Autumn	7	35	3	17
	Winter	2	6	4	3
1983-1984	Annual	26	74	24	30
	Spring/summer	26	69[a]	16	28
	Autumn	7	7	9	1
	Winter	1	9	1	1
1984-1985	Annual	75	91	66	77
	Spring/summer	9	48	10	47
	Autumn	71	74	60	55
	Winter	5	33	6	4
1985-1986	Annual	63	81	53	52
	Spring/summer	2	78	1	3
	Autumn	53	13	52	50
	Winter	0	0	0	0
Mean	Annual	55	82	48	53
	Spring/summer	10	65	9	26
	Autumn	35	32	31	31
	Winter	2	12	3	2

[a] Rates for fawns are calculated for summer only.

mortality rates averaged 31% for both both males and females (Table 8). Numbers of adult females declined an average of only 3% during winter and adult males declined only 2%.

Hunting was the primary cause of death among marked females, accounting for 17 (89%) of 19 deer lost from the population during autumn (Table 9). Seven (41%)

Table 9. Number of marked white-tailed deer lost from the Cherry Creek population by season, 1983-1987.

				Cause		
Sex	Age	No. alive	Season	Hunting	Natural	Total
F	0	4	Winter	0	1	1
M	0	4	Winter	0	0	0
F	≥1	28	Summer	0	2[a]	2
			Autumn	17	2[b]	19
			Winter	0	0	0
M	≥1	5	Summer	0	5[c]	5
	Total	41	All	17	10	27

[a] Both females dispersed from the area.
[b] One female dispersed from the area.
[c] Four males dispersed from the area.

of these deaths resulted from crippling or were illegal kills. On a yearlong basis, 81% of the 21 marked adult females that died were shot by hunters.

Population declines during 1983-1986 appeared to be influenced largely by low fawn recruitment combined with high adult mortality during autumn. However, continued decline in total numbers from spring 1986 to spring 1987 may have been at least partially attributable to changes in distribution among whitetails on the area in winter and spring. Five radio-collared females remained in the population during winter 1986-1987. All normally wintered on the study area as indicated by the fact that 92 (84%) of 109 relocations during 1983-1986 were within survey area boundaries. This compared to only 2 (23%) of 13 locations recorded in winter 1986-1987 within the area. The shift in distribution observed for those individuals also may have occurred for the population as a whole because most white-tailed deer remaining in the population by autumn 1986 were found on that portion of the study area included within the home ranges of these 5 radioed females.

Immigration and Emigration

Because whitetails, like mule deer, were marked only on the study area, we were able only to detect emigration. Movements of the small sample marked on the area suggested a relatively high incidence of emigration among young animals. All four males marked as fawns were observed regularly through winter but disappeared during June, the time when emigration begins (Nelson and Mech 1984). No mortalities of marked or unmarked deer were observed during this period. Three of five collared female fawns also emigrated, two apparently as yearlings and one as a 3-year old. No marked females older than 3 years emigrated.

As noted above, both population trends and "mortality" rates of white-tailed deer indicated high net losses of adults during summer. In the absence of direct evidence of mortality to account for these losses in most years, we suspect that high rates of emigration exceeding immigration may be characteristic of the population, at least during years or periods of high density and recruitment.

Factors Influencing Population Dynamics

The dynamics of any animal population can be described by rates of birth, death, immigration, and emigration over time. In this study, populations of both species increased, coincident with high fawn production and survival, from the mid-late 1970s through peaks during 1982-1984. They declined significantly during 1983-1986 concurrent with reduced recruitment and relatively high adult mortality.

Hunter harvest was a major factor influencing deer population dynamics on the study area.
(Photo by: Montana Department of Fish, Wildlife and Parks)

Preliminary analyses suggested that three major population and environmental factors or variables could have influenced these trends — population density, weather, and hunter harvests. Two others, including disease (periodic outbreaks of EHD) and possibly behavior-influenced dispersal, may have been important periodically, especially in white-tailed deer. Although some incidence of predation was observed, and potential existed for interspecific competition between mule deer and whitetails, and between these species and domestic livestock, neither appeared significant or of overriding importance in population dynamics of deer during the study.

Mule Deer

Density.—Population theory for mammals and most management models for deer assume that animal density is a primary variable affecting population dynamics. As population size increases, density-dependent responses (usually competition for food) progressively limit population growth by reducing animal condition, decreasing reproduction, and increasing mortality until population growth ceases. Decreases in deer numbers in this density-dependent model are accompanied by decreasing mortality and increasing reproduction until population growth resumes or stability is achieved.

Because of possible concern about the precision of population estimates and composition during 1975-1982, we statistically evaluated density relationships in terms of mortality rates only through the period 1982-1987. Data were most complete and precise and the population peaked and declined significantly through that period.

In contrast to the pattern normally expected for ungulates (Caughley 1976), mortality rate of fawns during summer was negatively correlated with numbers of fawns, females, and total deer ($r = -0.96$, $n=5$, $P<0.01$). That is, when densities were high fawn mortality rates were low. This negative density relationship also was evident in general patterns of reproduction and recruitment during the years of population growth after 1975; most seasonal fawn:doe ratios increased to highs as population size and density approached peaks during the early 1980s.

None of this implies a cause-and-effect relationship between high population density and low fawn mortality. Instead, it indicates that deer numbers or density *per se* was not a major factor influencing declining fawn recruitment that occurred from autumn 1983 through spring 1986. It also indicated that there were no "compensatory" decreases in fawn mortality nor compensatory increases in fawn recruitment rates resulting from reduced mule deer densities.

Fawn mortality varied widely among years, but was not directly influenced by deer numbers or density on the study area. *(Photo by: Alan K. Wood)*

Among adults, only mortality rate of adult females over summer was correlated with population density. During 1982-1986, summer mortality among adult females was highest when female densities were highest and decreased with density thereafter ($r=0.86$, $n=5$, $P=0.06$). Although this suggested that mortality rates of adult females might have responded in a more traditional manner to changes in population density, we found no correlation between natural mortality rates and density for females during winter or for males during any season. Thus, the relationship observed for summer may have been related to emigration.

Skogland (1983) proposed that increasing ungulate population densities result in decreasing physical condition of individuals in the population. Hanks (1981) suggested that such a decrease in physical condition leads to the following sequential demographic changes: 1) increased juvenile mortality, 2) increased age at sexual maturity, 3) decreased fecundity of mature females, and 4) increased adult mortality. Mule deer on Cherry Creek did not respond in this fashion to increased density. Fawn mortality rates increased with decreasing density, average litter sizes decreased as density decreased, and natural mortality rates of adults remained low and fairly stable (range 2-13%).

Weather.—Winter severity and other weather conditions varied through the study. Relative winter severity influences habitat and forage availability, the rate of fat utilization and ultimately overwinter mortality rates. The nutritional plane and condition of adult females during winter also may influence subsequent reproduction and neonatal mortality of fawns (Verme 1969). Annual variations in amount and timing of precipitation influences vegetation production in the northern plains. Precipitation during July-April prior to the growing season, determines the amount of soil moisture available for plant growth and directly influences herbage production (Rogler and Haas 1947, Blaidell 1958, Smoliak 1986, Hamlin and Mackie 1989). Together with temperature, it also influences the length of time that plants remain green and succulent, providing high quality forage for deer. Summer forage conditions can be critical to fawn survival, body growth and condition, and accumulation of fat reserves among adults.

Overwinter (Dec-Mar) fawn mortality rates of mule deer on the study area seemed to be influenced by winter severity, but the impact differed through the study (Fig. 7). Trends in overwinter fawn mortality followed those of winter severity only from 1982 to 1985 (r=0.94, *P*=0.03). During the remainder of the study, fawn mortality rates

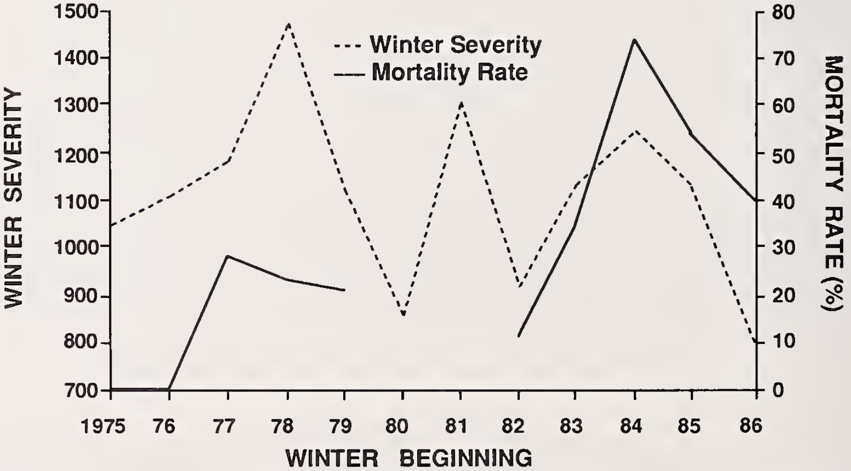


Fig. 7. Relationship between a modified Leckenby winter severity index and mule deer fawn mortality on the Cherry Creek area from November through March, 1975-1986.

during winter varied independently of winter severity. For example, the winter of 1985-1986 was very mild as compared with others during the study, yet fawn mortality was relatively high (41%). Conversely, winter 1977-1978 was very severe, but fawn mortality was only 23%. Winter 1978-1979 also was quite severe, but fawn mortality was relatively light. In addition, fawn:doe ratios for autumn and early winter following those two most severe winters were the highest observed during this study (Table 3). Winter mortality rates of adults also were low during those winters.

These data indicated that winter severity and associated habitat and forage restrictions alone were not significantly limiting fawn or adult survival. Rather, it appeared that range conditions during the previous summer may have been important. Average or greater precipitation during 1975-1978 probably resulted in relatively good summer forage conditions during those years. Thus, deer entering winters 1977-1978 and 1978-1979 should have been in good condition with ample fat reserves to carry them through those severe winters. On the other hand, relatively high overwinter mortality rates among fawns from 1983-1984 through 1985-1986 (Fig. 7) were associated with extreme drought and poor summer forage conditions that prevailed from 1983 through late summer 1985 (Fig. 2). Although sample sizes were small, measurements of dressed weights, antler size, diastemae of the lower jaw of yearling males, and kidney fat all indicated that body condition declined during 1983-1984 (Wood 1987).

The apparent relationship between summer forage conditions and fawn survival was further evidenced by significant correlations between the total amount of precipitation occurring in the area from July through April prior to fawning and percent fawns in the population the following winter ($r=0.75$, $P=0.01$) and spring ($r=0.76$, $P=0.01$). Similar significant correlations between precipitation and fawn survival have been documented for mule deer in the Missouri River Breaks, where July through April precipitation was closely correlated with subsequent forage production on transects (Hamlin and Mackie 1989).

Relationships between forage production and fawn survival are seldom a direct response to the amount of forage produced. For example, Smith and LeCount (1979) suggested that correlations between fawn:doe ratios and herbaceous growth resulted from increased vegetative cover that limited predation as well as from increased forage production. Hamlin and Mackie (1989) reported relationships between weather patterns, forage production, and winter fawn:doe ratios in central Montana. However, fawn recruitment was not tied to forage quantity because forage supplies could support many more deer than were present. Similar forage surpluses during summer also have been documented elsewhere (Wallmo et al. 1977). Hamlin and Mackie (1989) speculated that the actual response in fawn survival resulted from improved forage quality and the length of time succulent forage was available rather than quantity.

Forage quality, as influenced by nutrient content and digestibility, could limit productivity by influencing physical condition of females and their ability to support young. Several studies have demonstrated relationships between precipitation or forage production on summer ranges and herd productivity or population fluctuations. These relationships have been reported among mule deer populations (Julander et al. 1961, Pederson and Harper 1978, Smith and LeCount 1979), as well as other big game species that inhabit semiarid environments (Marburger and Thomas 1965, Anthony 1976, Wehausen et al. 1987). They could all be a response by the animals to forage quality on summer ranges.

Similar interpretations also may apply to the correlations described above for mule deer on our study area. Fawn mortality through summer is influenced by physical condition of the doe (Verme 1969). However, physical condition of adult females is a function of previous physical condition and past reproductive history (Mundinger 1982, Dusek et al. 1987, Hamlin and Mackie 1987) as well as forage quality during summer. Consequently, autumn fawn:doe ratios are not necessarily related directly to precipitation and forage quality because fawns are nutritionally dependent on their mothers through most of the summer. Fawn survival during late summer and autumn should be more influenced by forage quality as fawns become nutritionally independent. Body growth and fat accumulation also can influence fawn

Table 10. Hunting regulations for the hunting district that included the Cherry Creek study area, 1975-1986. Unlimited licenses could be purchased by resident hunters; limited permits were issued through drawings.

Year	Unlimited licenses	Limited permits
1975	1 ES[a] ESp. + 1 ES WT	
1976[b]	1 ES WT	50 ES MD
1977	1 ES WT	200 antlered MD
1978	1 ES WT or antlered MD	none
1979	1 ES WT or antlered MD	200 antlerless WT
1980	1 ES WT or antlered MD	200 antlerless ESp.
1981	1 ES ESp.	200 antlerless WT
1982[b]	1 ES ESp.	none
1983	1 ES ESp.	200 antlerless ESp.
1984[b]	1 ES ESp. + 5 antlerless WT	5,000 antlerless ESp.
1985	1 ES ESp. + 1 antlerless WT	4,000 antlerless ESp.
1986	1 ES ESp. + 1 antlerless WT	none

[a] ES = either sex deer, ESp. = either species of deer, WT = white-tailed deer, MD = mule deer.

[b] Hunting district boundaries were changed in these years so number of permits issued was not comparable to previous years.

survival rates through winter. Thus, forage quality may have a more direct effect on fawn survival to winter and spring than through summer.

Hunting.—Hunting was the most important mortality factor among adult mule deer during 1982-1986. Overall, harvest rates were influenced primarily by the hunting regulations applied.

Regulations varied from 1975 to 1986 (Table 10) and were generally more conservative during earlier years and more liberal during later years. Antlerless mule deer were not legal game during 1977-1979. However, in 1980, a limited number of permits was issued to allow harvest of antlerless mule deer. In 1982 hunters were authorized to take one deer of either sex or species, resulting in harvest of about 1% of the adult females on the area (Table 4). Special regulations were implemented in 1983 allowing hunters to take additional antlerless deer of either species with "B" tags (Table 10). From 1983 through 1985, respectively, 6.2, 27.7, and 22.2 "B" tags were sold/100 km^2 of hunting district. They resulted in harvest of 9, 37, and 27% of the estimated numbers of adult female mule deer on the study area at the onset of hunting in autumn 1983, 1984, and 1985, respectively. The harvest rate of adult females during 1986 (31%) was slightly higher than 1985, even though extra antlerless permits were not authorized for mule deer.

Harvest rates of adult males reflected intense selection by hunters for males with large antlers, as described by others (Taber and Dasmann 1957, Robinette et al. 1977, Barlow and McCulloch 1984). Yearling males were more vulnerable to hunters than mature males but hunters even exhibited a selective harvest among yearlings. During 1983 and 1984, yearling males with at least 2 points on each antler were harvested at rates of 80-87% (as indicated from change-in-ratio procedures), whereas those with at least 1 unbranched antler (spikes) were harvested at rates of only 15-36% (Table 11). The increased harvest of spikes during 1984 probably resulted from their harvest as "antlerless" deer and their increased abundance. Antler beam lengths of only 4 cm

Table 11. Estimated percentage of the preseason population of mule deer that disappeared from the Cherry Creek area during the hunting season, 1982-1986.

				Adult male				
						Yearling		
Year	Total	Fawns	Adult female	All	Mature	All	2-point	Spike
1982	10	0	1	62	60	63		
1983	19	9	9	59	73	48	87	15
1984	45	45	37	65	71	61	80	36
1985	31	28	27	48	48	50		
1986	30	17	31	58	63	42		

were measured on 2 yearling males shot by hunters in 1984, antler beam lengths decreased an average 14%, and the percentage of all yearlings that were spikes increased by 37% from 1983 to 1984 (Wood 1987).

Harvest rates of adult males were similar to the 56% harvest rate reported in Utah by Robinette et al. (1977) and were much higher than the 15% reported in Arizona by Barlow and McCulloch (1984). Harvest rates of males on Cherry Creek were higher than annual mortality rates of 24-29% reported in California by Taber and Dasmann (1957). Harvest rates for adult females were comparable only to the 19% reported in Utah (Robinette et al. 1977). Higher annual harvest rates for mule deer have been reported only from studies on the National Bison Range in western Montana where 50% of the adults were removed (Nellis 1968).

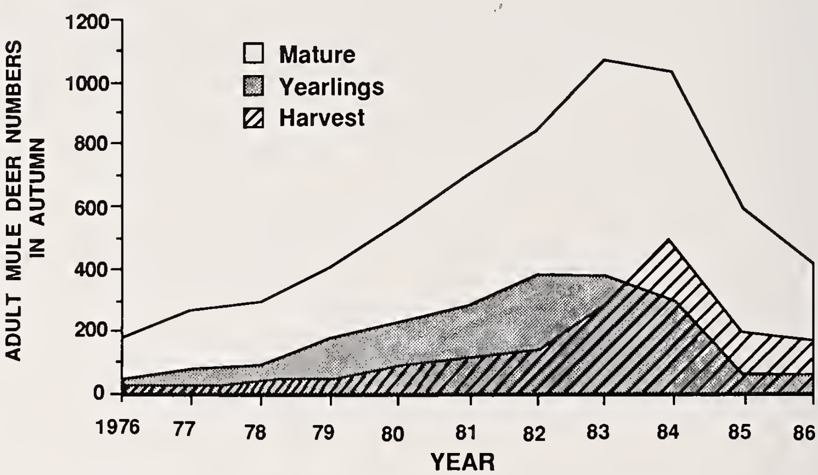


Fig. 8. Number of yearling and mature (≥ 2 years) mule deer during autumn, and total autumn harvest of adults on the Cherry Creek area during 1976-1986.

As indicated by seasonal population estimates and harvest regulations, harvest rates were lower than rates of recruitment of yearlings into adult populations throughout the years of population increase. From 1976 to 1980, the population averaged 37% fawns during spring. This resulted in a steady increase in the number of adults in the following autumn. Declines in numbers of adults from 1984 through 1986 resulted from decreases in numbers of yearlings in the population concurrent with increased harvests (Fig. 8). These data indicate that the 21% average annual harvest of adult females during 1982-1986 was not sustainable because fawn production and recruitment was low and did not increase to compensate for adult mortality. Eustace and Swenson (1977), and Swenson (1978) suggested that previous mule deer population declines in eastern Montana also resulted from a combination of declining recruitment and increased harvests.

There were no compensatory decreases in natural mortality rates resulting from increased harvests during 1982-1987. In fact, the trends in all data indicated concurrent increases in natural mortality and harvest rates for fawns and adult females (Fig. 9). Compensatory decreases in natural mortality rates with increasing harvests are a common assumption in wildlife management, and have been proposed

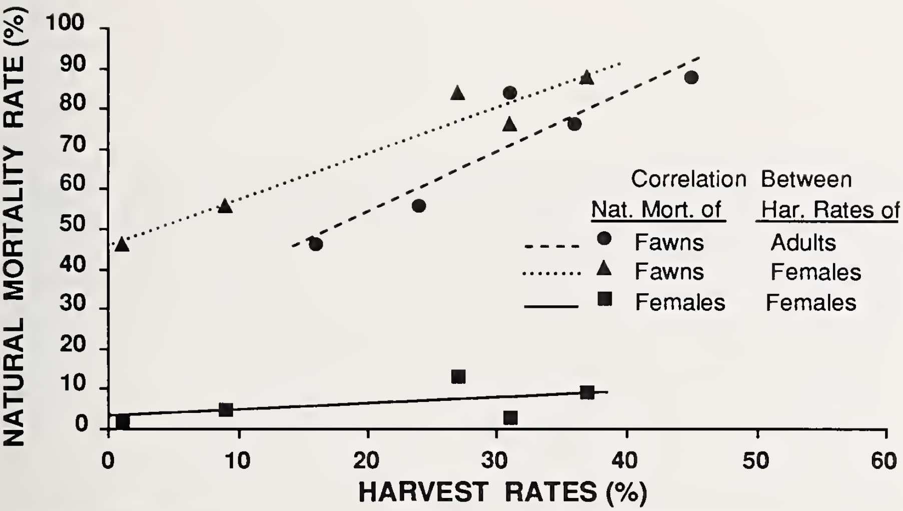


Fig. 9. Relationships between harvest rates and annual natural mortality rates of mule deer on the Cherry Creek area, 1982-1986.

specifically for North American big game by McCullough (1979) and Houston (1982). Even if compensatory mortality can be demonstrated it is unreasonable to assume that hunting mortality could completely replace natural mortality in wild ungulate populations (Caughley 1976).

Numbers of adult males harvested were positively correlated with numbers of adult males in the autumn population from 1982 through 1986 ($r=0.991$, $P<0.001$). Total mule deer harvests on a 7,750 km^2 area surrounding the study area also were correlated with numbers of adult mule deer on the study area at the start of each hunting season ($r=0.982$, $P<0.01$) from 1977 through 1982. This relationship did not continue after 1982 because changes in hunting regulations increased antlerless harvests as discussed previously.

Swenson (1982) also reported a positive relationship between deer harvest and observed deer density among all nonforested hunting districts in southeastern Montana. Factors such as hunting pressure, hunting regulations, and weather also may influence hunter harvests (Freddy 1982). However, the findings of this study and Swenson (1982) both indicate that mule deer occupying open habitats are extremely vulnerable to hunters regardless of other factors. Harvest rates of adult males were independent on the density of adult males even at very low densities (0.15 males/km^2 during 1986). Thus, any security threshold that may exist appears to be very low in nontimbered prairie habitats.

White-tailed Deer

Assessment of factors influencing population dynamics and trends of whitetails on the study area was hampered by incomplete population data, small samples of marked deer during 1982-1986, and lack of detailed information on some factors.

Several factors including weather, hunting, EHD, and emigration probably were involved in population trends from 1975 through 1982, though detailed data were not obtained. For example, EHD outbreaks on and near Cherry Creek during the summers of 1976, 1977, and 1978 (Walcheck 1978) may have contributed to the declining whitetail population (Fig. 6) during those years. About 33% of all whitetails on the Yellowstone River, located 85 km to the east, died from EHD during 1977 (Swenson 1979).

Outbreaks of epizootic hemorrhagic disease (EHD) may occasionally influence numbers of white-tailed deer in prairie environments. *(Photo by: Alan K. Wood)*

Overwinter mortality of approximately 29% occurred during January-April 1978 and coincided with relatively severe winter weather (Fig. 3). Although the winter of 1978-1979 was even more severe, it seemed to have less impact on overwinter fawn survival and no adverse impact on subsequent fawn production. The population declined only 6% over this winter and subsequently increased to approximately 230 in spring 1980. There was no correlation between winter severity and percent fawns in spring. It seemed that severe winter weather may impact population size but the effect is probably variable as it was for mule deer.

Total precipitation received prior to fawning season (July through April) was correlated with percent fawns in winter ($r=0.69$, $P=0.04$) and spring ($r=0.78$, $P=0.01$). It seemed that drought conditions affected whitetails in a manner similar to mule deer. Low overwinter mortality rates for adult whitetails and high proportions of fawns following severe winters suggested that whitetails also had access to suitable winter ranges.

Increased hunting pressure directed toward whitetails from 1976 to 1980 also may have influenced population size during this period. During 1976-1977, most hunters could shoot only whitetails. Hunters could shoot any whitetails but only antlered mule deer from 1977 through 1980 (Table 10). This disproportionate hunting pressure contributed to stabilizing whitetail populations and might have been a factor influencing mule deer population increases (Fig. 5). Increased fawn survival and possibly lowered mortality rates for adult females probably contributed to population growth from 1980 through 1983. Higher rates of population decline over summer at higher population densities from 1983 through 1985 also suggested the possibility of a density dependent response influencing population size through emigration during summer.

Whitetail population trends during 1982-1986 were influenced primarily by two factors: increased harvests resulting from liberal hunting regulations (Table 10), and decreased fawn survival. Increased harvest rates appeared to be the primary factor. Antlerless deer "B" tags (6.2 tags/100 km^2) were valid for either species in addition to an "A" tag in 1983, and harvest rates were relatively low (9% for adult females, 1% for adult males). Each hunter could purchase up to 6 deer tags in 1984. These more liberal permit quotas directed hunting pressure specifically at antlerless whitetails (24.7 tags/100 km^2) and resulted in a harvest rate of 60% for adult females and 55% for adult males. This was a 6-fold increase in the female harvest over 1983. Unlimited numbers of permits were available during 1985 but each hunter was allowed only one. Although this restriction resulted in a decreased harvest rate (52% for adult females and 50% for adult males) compared to 1984, the harvest rate during 1985 was still 5-times greater than during 1983.

Creed and Kubisiak (1973) reported that hunters were able to shoot the entire population of 544 white-tailed deer in 44 days during an experimental deer hunt in central Wisconsin. They felt that hunter persistence, heavy hunting pressure, good access, and patchy wooded areas all contributed to the ability of hunters to eliminate this population. We believe the same factors also promoted increased harvests on Cherry Creek. It is obviously possible for wildlife managers to use hunting regulations to reduce whitetail populations that occupy open, patchy habitats even though the behavior of deer may change in response to heavy hunting pressure (Sparrowe and Springer 1970).

HABITAT USE

Mule Deer

Distribution

Mule deer on the study area occurred in an aggregated pattern typical of animals occupying patchy environments. They were observed in only 37% of the 2,172, 25-ha cells covering the study area during all survey flights from 1975 through 1986. Only 20, 19, and 15% of the cells were occupied during autumn, winter, and spring, respectively. Density distribution also indicated aggregated distribution. During peak populations in December 1983, density averaged 2.3 deer/km^2 across the entire area, but local concentrations ranged from 5 to 33 deer/km^2.

The general pattern of dispersion, illustrated by the distribution of mule deer groups observed during winter surveys from 1975 through 1985, is presented in Figure 10. Greatest concentrations and most continuous distribution occurred along the Yellowstone-Missouri drainage divide. Local areas of relatively high density were interspersed among vacant or low density areas.

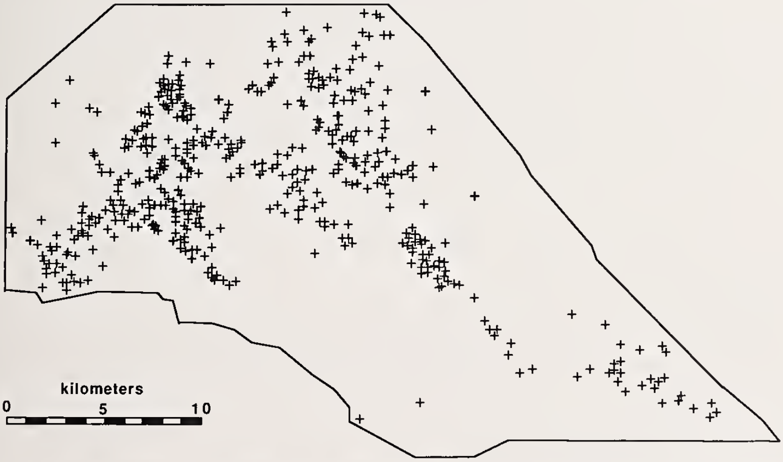


Fig. 10. Distribution of mule deer groups observed on the Cherry Creek study area during aerial surveys in winter, 1975-1985.

There were no major changes in distribution associated with increases in mule deer numbers from 1975-1980, when population density was relatively low, to 1982-1983 when density peaked. Deer seasonally used the same areas (25-ha cells) more than expected during both periods and used new cells less than expected during the population high ($P<0.05$). Apparently, the availability of suitable habitat was sufficiently restricted and initial deer density was sufficiently low that population growth occurred almost entirely within initially occupied habitat.

Mule deer were most widely dispersed during summer and autumn and became increasing aggregated during winter and spring as indicated by numbers of cells in which deer were recorded during aerial surveys. In part, these seasonal changes reflected behavioral attributes of mule deer. Deer were most widely distributed during summer when group sizes were small and mature females isolated themselves during parturition and fawn rearing (Wood 1987); they increased during autumn and winter as family groups combined. However, aggregation also increased as availability of forage and other needed resources declined and deer made common use of the most favorable habitats.

There was some evidence of spatial segregation between mature males and females. The number of males observed per 25-ha cell during surveys decreased as the number of females per cell increased (r_s=-0.29, *P*<0.001) during each summer or autumn survey. The number of fawns per cell, which should represent habitats capable of supporting reproductively successful females, was even more negatively correlated with the number of mature males (r_s=-0.55, *P*<0.001). Although the negative association between males and reproducing females was not particularly strong, it was stronger than the positive association between females and fawns (r_s=0.42, *P*<0.001). This indicated that mature males generally avoided areas occupied by females with fawns. Most of the overlap that occurred between mature males and females involved use of common feeding areas such as agricultural fields and/or habitats used in common with nonreproductive females. Sexual segregation, or occurrence of "buck habitats", has been reported among deer in other environments (Mackie 1970, Bowyer 1984, Ordway and Krausman 1986).

The general pattern of dispersion, combined with traditional patterns of movement and use of specific areas suggested that aggregations associated with different portions of the area comprised subpopulation units. These units probably consisted of matrilineal groups with overlapping ranges. Those separated by unoccupied habitat were most discrete, whereas subpopulations that occupied more continuous patches of preferred habitats exhibited more overlap, especially during summer and autumn.

General Movement Patterns

Eighty-six (78%) of 110 marked females were observed frequently enough to identify individual movement patterns. Three distinct patterns were apparent: 25 (29%) were yearlong residents, 45 (52%) were summer migrants, and 16 (19%) were autumn migrants.

Although yearlong residents may use different parts of their home range disproportionately during different seasons, their movements were not patterned in a manner that justified delineation of seasonal ranges (Fig. 11). They did not exhibit any consistent seasonal shifts in elevation or centers of activity.

Summer migrants exhibited typical spring and autumn movement between distinct summer and winter ranges (Fig. 11). This migratory pattern differed from that described for mule deer in most mountainous habitats only in the direction and amount of elevational change involved. During spring, summer migrants moved downward in elevation (mean, 72 m; range, 15-130m) from winter ranges in badlands to summer ranges in sagebrush grasslands and mesic shrublands. The average distance between individual centers of activity on winter and summer ranges was 5.9 km (range, 1-80 km). Spring migration usually occurred in late March or April; return to winter range occurred between mid October and late December. Individual deer completed the migration in less than 8 days, the average interval between relocations. One adult doe was known to complete the move overnight.

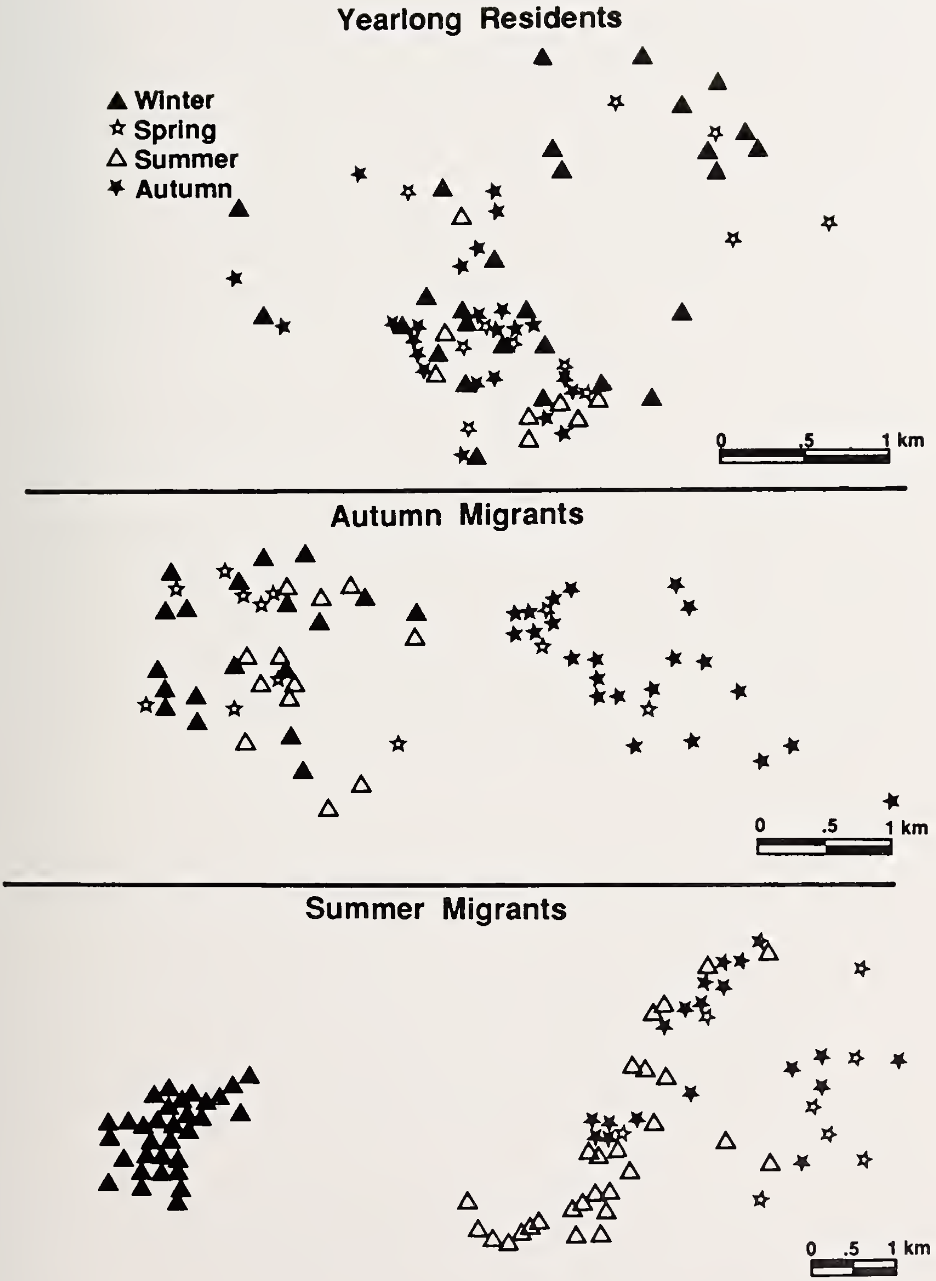


Fig. 11. Locations of selected female mule deer illustrating contrasting patterns of seasonal home range use by summer migrants, autumn migrants, and yearlong residents on the Cherry Creek area, 1983-1987.

Martinka (1968) reported that mule deer in foothills of the Bear Paw Mountains of northern Montana similarly migrated downward in elevation in spring and upward in winter, but did not quantify the elevational change or distance moved. Hamlin and Mackie (1989) found both yearlong resident and migratory mule deer in the Missouri River Breaks. Migrants moved 3-9 km between summer habitats in drainage heads with low topographic relief to steeper, vegetatively more diverse terrain during winter. Although winter ranges were "lower" in the Missouri River Breaks, little elevational change was involved.

Autumn migrants included deer that remained on 1 home range from late autumn to late summer and moved to an alternate home range occupied from approximately mid August to mid October (Fig 11). Average distance between activity centers of deer on the 2 ranges was 2.9 km (range, 1.5-6.0 km). Autumn migrants also moved downward in elevation (mean, 69 m; range, 30-170 m) from winter, spring, and early-mid summer ranges within badlands to habitats with an increased component of mesic shrubland and sagebrush grasslands.

Other studies in the northern plains have described similar movements of mule deer to more mesic habitats during late summer-autumn (Martinka 1968, Mackie 1970, Dusek 1975), but they were not considered migrational. The movements of both summer and autumn migrants on the Cherry Creek area were typical migrational movements according to Baker's (1978) characterization: (1) subsequent return to the original habitat (2) geographical directionality (3) periodicity, and (4) some distance separating the ranges. Most migrants were easily identified because seasonal ranges were distinct and separated by large distances. When distances were shorter and seasonal ranges less distinct, timing and direction of home range shifts were used to help classify movement patterns. Recent studies of desert mule deer (Rautenstrauch and Krausman 1989) have similarly distinguished individuals with distinct winter and summer dry season home ranges as migratory.

Monthly Movement Patterns

Females classified as yearlong residents, summer migrants, and autumn migrants exhibited significant differences ($P<0.001$) in monthly average activity radii (AARs) (Fig. 12). This supported the original classification and suggested that the 3 groups followed different strategies in utilizing habitat resources available on the study area.

Mean monthly AARs of resident females were relatively constant throughout the year, except for a slight decrease during fawning season and increases during September and November. Autumn movements of residents were nondirectional. The increase during September followed and presumably was influenced by desiccation of herbaceous forage, whereas that in November probably resulted from disturbance by hunters.

Movements of autumn migrants increased slightly, though nondirectionaly, during spring, decreased during the fawning season, then increased through autumn. The peak during November probably reflected the combined effects of seasonal change in habitat use, migration, and disturbance by hunters.

Movements of summer migrants were typical of animals with seasonal migrations. The increase during July resulted from unusual movements by 2 yearling females and 2, 2-year-old females in 1983. The pattern for summer migrants was a stable AAR from May through September when these 4 monthly values were excluded.

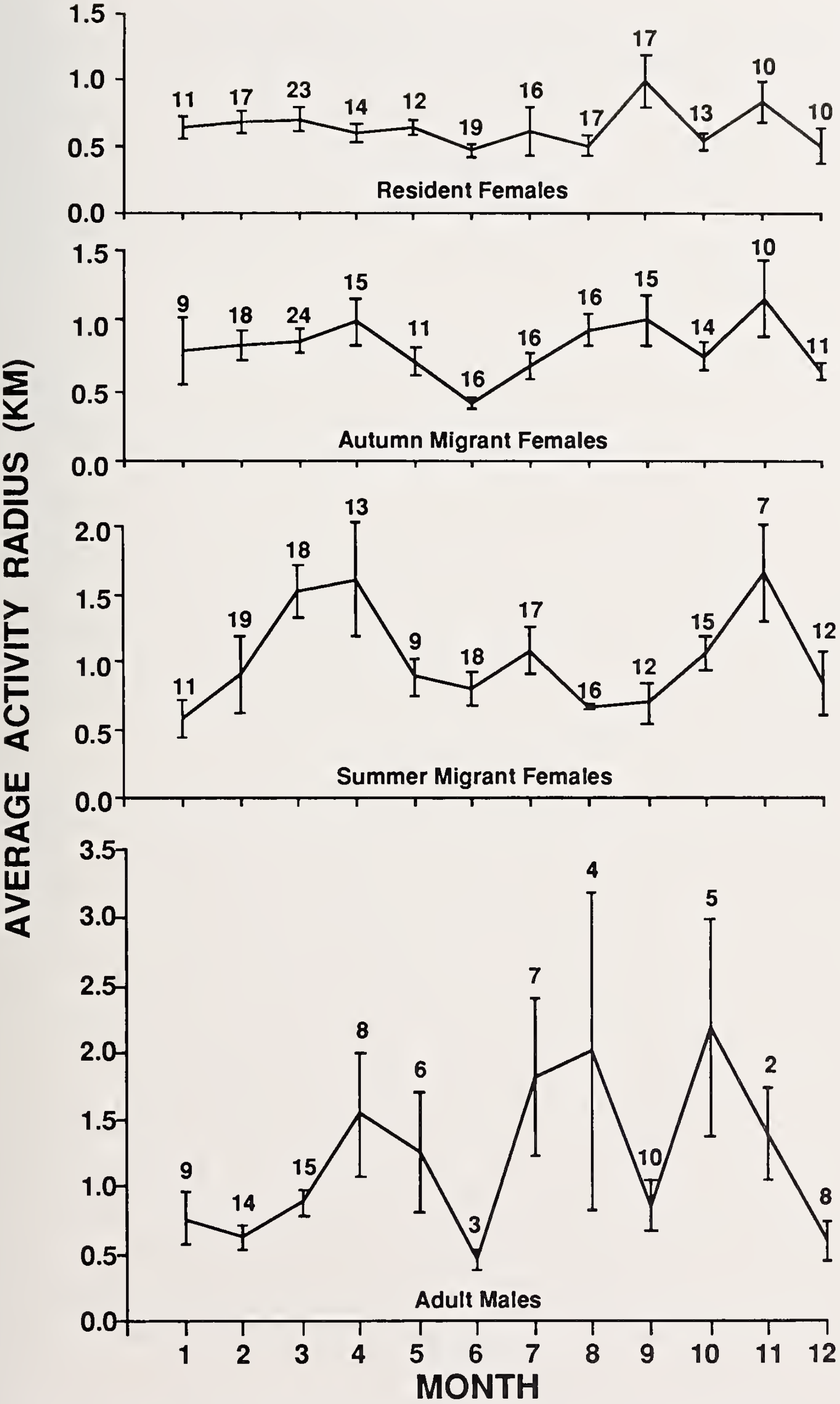


Fig. 12. Monthly average activity radius (mean ± SE) for each female migration class and adult males on the Cherry Creek area, 1983-1985. Numbers of deer are recorded above each month.

AARs of males were plotted for comparative purposes only because data were insufficient to statistically contrast the movements of radioed females and neck-banded males. Males exhibited extreme variations in movement that were similar to females only through winter and during June (Fig. 12). The increase during July resulted from long movements by 2 yearling males that later returned to their original locations, and the increase during August from movements associated with the emigration of another yearling male. The movement pattern for adult males was most similar to that exhibited by summer migrant females when these extreme movements were excluded.

Seasonal Home Range Size

Among deer, seasonal movements and home range size may vary widely in relation to the general nature and diversity of habitats occupied (Mackie et al. 1980). This appeared to be the case on the Cherry Creek area where seasonal AARs and polygon home ranges (PHRs) generally differed among individual females following different migration patterns (Table 12).

Among adult females, individual AARs varied from 0.36 to 1.76 km during summer and 0.32-1.71 km in winter; PHRs varied from 0.52 to 6.15 km^2 and 0.48-13.65 km^2, respectively, during the two seasons. Sample sizes were adequate to calculate minimal home range size estimates for males only during winter, when individual AARs ranged from 0.50 to 1.32 km and PHRs varied 10-fold from 0.83 to 8.41 km^2. Differences in AARs and PHRs for individuals in summer and winter were not significant ($P>0.2$). Estimates of AARs for males during winter were not significantly different from those for any female group but PHRs were larger than both autumn migrant and yearlong resident females.

Females classified as summer migrants had significantly larger home ranges than yearlong residents ($P<0.05$) throughout the year (Table 12). Mean home range size of autumn migrants was intermediate between summer migrant and yearlong resident classes during summer and similar to yearlong residents during winter, though none of the differences in AARs or PHRs were significant ($P>0.05$).

Direct comparison of average home range size for adult females on the Cherry Creek area with estimates for other areas was hampered by differences in methods and sample sizes among studies reported in the literature. Also, our estimates, especially PHRs, probably were minimal because of the relatively small numbers of locations (9-32) per individual per season (Table 12). Studies have shown that polygon home range size tends to increase with sampling intensity (Anderson 1982).

Despite these limitations, our data indicated that females occupied home ranges that were at least intermediate-to-large relative to those in other habitats. In general, seasonal home ranges seem to be small among mule deer in mesic mountainous habitats (Hamlin 1974, Pac 1976, Harestad 1979, Schoen and Kirchhoff 1985) and large in more xeric, desert habitats (Rodgers et al. 1978, Eberhardt et al. 1984, Rautenstrauch and Krausman 1989). However, mule deer on the Cherry Creek area apparently had home ranges that were smaller than average for some mountain environments (Moir 1976, Nyberg 1980, Rosgaard 1981) and larger than average for some desert habitats (Dickinson and Garner 1979).

Seasonal changes in mobility, variability in movement patterns, and relative prevalence of each pattern may be more descriptive of a population's ecology than a simple description or comparison of average home range size. Other studies (Harestad

Table 12. Estimates of average activity radius (AAR) and polygon home range size for mule deer on the Cherry Creek area, 1983-1985. Within each season, mean AAR's followed by different capital letters were significantly different ($P < 0.05$).

Season and Migration class[a]	No. deer	No. points/ home range		AAR (km)			Polygon (km^2)		
		$\bar{X}$	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range
Study-long									
YR	23	44	22-78	0.85 A	0.05	0.52-1.62	6.30 A	0.61	1.83-13.64
AM	16	47	27-79	1.26 B	0.09	0.84-2.26	11.65 B	1.49	4.87-31.18
SM	31	43	23-78	2.37 C	0.14	1.21-5.12	20.59 C	2.28	9.11-65.99
Summer									
YR	16	15	10-22	0.63 A	0.05	0.36-1.08	1.63 A	0.27	0.52-4.83
AM	11	15	9-23	0.74 AB	0.09	0.38-1.16	2.08 AB	0.27	0.65-3.41
SM	17	14	9-26	0.94 B	0.07	0.56-1.76	2.88 B	0.36	0.70-6.15
Winter									
YR	31	17	10-29	0.74 A	0.06	0.32-1.71	2.29 A	0.27	0.48-6.36
AM	21	17	11-32	0.75 AB	0.04	0.33-1.13	2.32 A	0.21	0.64-3.83
SM	31	16	9-24	0.93 B	0.06	0.44-1.86	3.41 AB	0.54	0.97-13.65
MA	10	15	9-23	0.89 AB	0.09	0.50-1.32	3.64 B	0.72	0.83-8.41

[a] YR = yearlong resident, AM = autumn migrants, SM = summer migrants, and MA = adult males.

1979, Loft et al. 1984, Schoen and Kirchhoff 1985, Rautenstrauch and Krausman 1989) also have identified multiple strategies used by deer to exploit a particular environment. Prairie environments offer diverse opportunities for successful occupancy of available habitat; high mobility and variable movement and home range pattern may be an important behavioral adaptation for exploiting those opportunities.

Home Range Fidelity

Adult females characteristically occupied the same individual home range areas within the same herd range from year to year. Fidelity to the same discrete area often was expressed in consistent use of a single branch of a drainage system. This was illustrated by locations of 4 marked deer observed from January 1983 through March 1985 (Fig. 13). Although those deer had overlapping winter ranges (upper end of drainage) and made common use of an alfalfa field at the confluence of the 2 branches, each essentially restricted all of its movements to either the upper or lower branch.

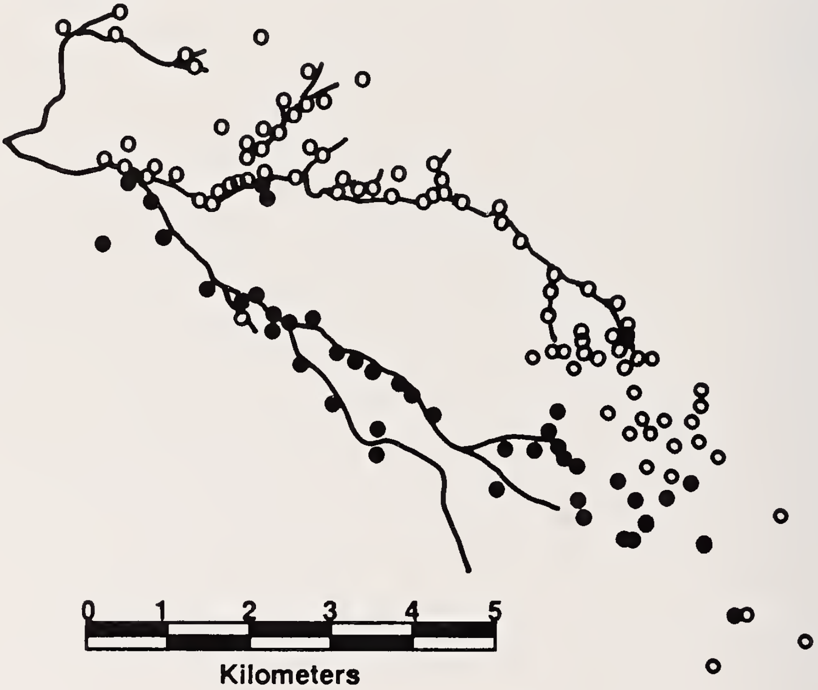


Fig. 13. Locations of four female mule deer on the Cherry Creek area from January 1983 to March 1985, illustrating fidelity of females to individual branches of a drainage system. Solid dots represent locations of 2 deer that resided in the lower fork and open circles the locations of 2 deer that resided in the upper fork of the drainage.

Other studies also have found mule deer to exhibit traditional use of individual home and herd range areas. Taber and Dasmann (1958) indicated that blacktails would move to areas with high quality forage within their home range but not to areas outside their home range no matter how good the food supply. Robinette (1966) reported a situation where deer temporarily shifted their home range 3-5 km in response to a wildfire on their winter range but returned when the vegetation recovered.

Emigration Movements

Emigration was defined as any movement out of an area larger than the home range with no expectation of a subsequent return (Bunnell and Harestad 1983). As discussed earlier, only 7 emigrants (3 females and 4 males) were confirmed among the 110 females and 67 males that were marked (Table 13), although another 13 male fawns also were classified as emigrants because of the time and pattern of

Table 13. Timing and distance moved by 7 mule deer that emigrated from their presumed birth range on the Cherry Creek area.

Sex	Age at dispersal	Date last observed on birth range	Date first sighted on new range	Dispersal distance (km)
F	1	04-28-83	09-23-83	12
F	2	05-30-84	08-01-84	26
F	6	12-21-84	09-17-86	24
M	1	08-16-83	08-19-83	11
M	1	03-08-83	12-29-83	140
M	1	06-19-83	08-15-83	19
M	2	03-29-85	11-08-86	35

disappearance. All but 1 of the documented cases resulted from observations of marked deer rather than hunter returns of neckbands. Also, emigration usually occurred only among yearlings or 2-year olds. The only older deer known to have emigrated was a 6-year-old female that disappeared from the study area in late December 1984 and was subsequently located on a "new" home range approximately 24 km from her original range in autumn 1986.

Emigration distances ranged from 12 to 26 km for females and 11-140 km for males (Table 13). Most other studies have reported shorter movements. Bunnell and Harestad (1983) concluded that movements greater than 12 km were rare in Washington and British Columbia, and Robinette (1966) reported that only 14% of emigrating males and 9% of emigrating females moved farther than 10 km. In contrast, Severson and Carter (1978) documented 17 mule deer that emigrated an average of 71 km from their South Dakota study area.

Longer movements may be more characteristic in patchy environments where suitable habitats are widely separated. This conclusion also is supported by the fact that 2 of the longest distances ever recorded (240 km by Robinette 1966, and 180 km by Severson and Carter 1978) were across areas offering little or no cover for deer. Mule deer distribution in the plains typically centers in widely scattered areas of rough topography (Severson 1981), surrounded by areas of marginal or non-deer habitat. In such areas, a deer leaving its natal area may have to travel a great distance before reaching other suitable, vacant habitat. Patchy deer distribution in the plains also might lead to higher rates of emigration because deer from "core" habitats can move into and across surrounding areas without encountering other deer as suggested by the "social fence" hypothesis (Hestbeck 1982).

Habitat Selection

Seasonal patterns of habitat use and selection, as determined by aerial surveys of mule deer throughout the study and relocations of radio-collared females during 1983-1985, are shown in Table 14. Most differences between the two data sets resulted from relatively small samples of telemetry data showing no statistically significant pattern of habitat use, whereas larger samples from survey data indicated significant selection. However, contradictions in selection of legume hayfields probably resulted because these fields were used primarily during crepuscular or nocturnal periods and both methods probably underestimated their use. Although biases in habitat use due to group size have been reported (Gasaway et al. 1985), there were no differences

Table 14. Habitat use of mule deer on the Cherry Creek study area based on radio locations (1983-1985) and deer observed during aerial surveys (1975-1985). Data are percentage of observations occurring in each cover type and a selection coefficient indicating avoidance (A) or selection (S) (*P*<0.05), or use in proportion to availability (U) (*P*>0.05).

	Annual		Spring		Summer		Autumn		Winter	
Habitat	Radio	Survey	Radio	Survey	Radio	Survey	Radio	Survey	Radio	Survey
Mixed prairies	3 A	6 A	4 A	10 A	2 A	5 A	3 A	7 A	3 A	4 A
Grainfields	0 A	0 A	0 A	0 A	0 A	0 A	0 A	0 A	0 A	0 A
Hayfields	0 A	1 S	0 A	0 A	1 U	3 S	0 A	3 S	0 A	0 A
Sagebrush grasslands	9 S	10 S	10 S	6 S	12 S	19 S	13 S	20 S	5 U	4 U
Bunchgrass prairies	13 S	16 S	24 S	25 S	5 U	10 U	7 U	9 S	18 S	15 S
Badlands	35 S	44 S	18 U	45 S	25 S	24 S	38 S	21 S	50 S	62 S
Mesic shrublands	6 S	8 S	8 U	3 S	12 S	15 S	6 S	21 S	1 U	2 S
Hardwood draws	34 S	15 S	36 S	11 S	43 S	24 S	33 S	19 S	23 S	13 S
Total observations	1,777	10,115	262	2,958	645	545	230	2,772	640	3,839

(*P*>0.05) in mean group size of deer observed in surveys or by radio relocation during any season.

During spring, mule deer generally used sagebrush grasslands, bunchgrass prairies, hardwood draws, mesic shrublands, and badlands more than expected (selected) on the basis of their relative occurrence on the area. Mixed prairies, grainfields, and hayfields were used less than expected (avoided) (*P*<0.05, Table 14). Selection patterns between data sets differed only in degree of preference exhibited for mesic shrublands and badlands habitats; both were used in proportion to availability by radioed females. Spring was a period of transition from winter to summer habitat use, and patterns in early April when surveys were conducted may have been somewhat different from those of late April and May, which were included in data for radioed deer. Bunchgrass prairies received more use by mule deer during spring than any other season (Table 14, Fig. 14). With more bare ground and less litter (Wood 1987) and diverse topography, the bunchgrass prairies may provide early spring forage.

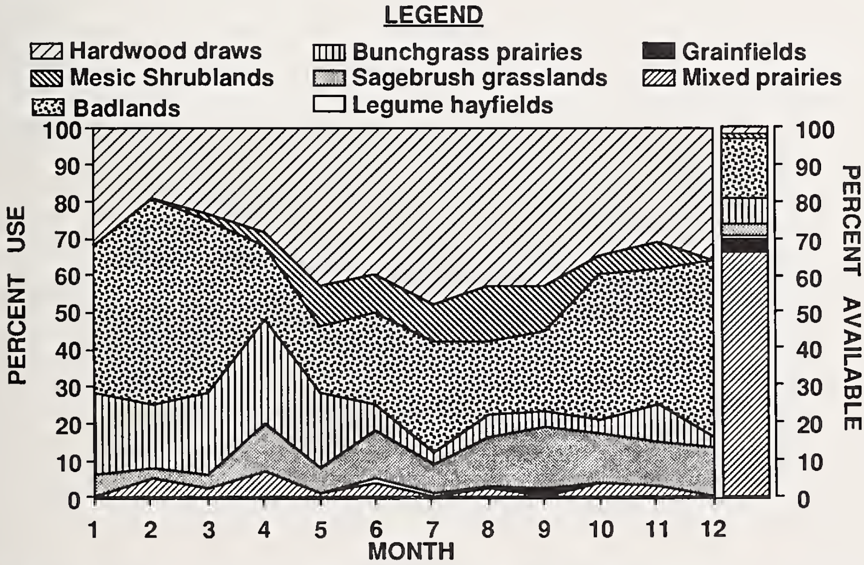


Fig. 14. Monthly patterns of habitat use by radioed female mule deer on the Cherry Creek area, 1983-1985, relative to habitat availability.

During summer, sagebrush grasslands, badlands, mesic shrublands, hardwood draws, and legume hayfields were selected; bunchgrass prairies were used in proportion to availability; and mixed prairies and grainfields were avoided (*P*<0.05, Table 14). Habitat use patterns based on data for radioed females were similar, except that legume hayfields were used only in proportion to availability. However, as noted above, both data sets may have underestimated use of these fields. Spotlight observations of deer on 2 areas with alfalfa fields indicated those fields were heavily used at night and highly preferred throughout the summer (*P*<0.001). Data for radioed females also indicated proportionately much greater use of hardwood draws than did survey data. This probably reflected both visibility bias against deer in habitat with overhead cover and differential selection by adult females for mesic habitats that provided both dense hiding cover and succulent forage while rearing fawns.

Summer habitat use patterns showed that deer preferred areas where vegetation remained green through late summer, indicating that availability of green, succulent forage was a primary factor in habitat selection throughout the period. Xeric badlands apparently were used only when closely associated with mesic shrublands or hardwood draws; those lacking inclusions of mesic habitats were virtually unused after July.

Habitat use during autumn was transitional between summer and winter patterns (Table 14, Fig. 14). Sagebrush grasslands, badlands, mesic shrublands, bunchgrass prairies, hardwood draws, and legume hayfields were generally selected; mixed prairies and grainfields were avoided ($P<0.05$). Data for radioed deer differed only in suggesting that bunchgrass prairies were used in proportion to availability and hayfields were avoided. Again, these differences may have been due to differences in the way that the two data sets were obtained. Survey data were obtained during early October, prior to the hunting season and onset of winter-like conditions, whereas radio relocations were made throughout October and November.

Swenson (1982) reported that mule deer used habitats providing more security during hunting season than those occupied either before or after the season. Hunting had little effect on habitat use patterns on our study area, even during years of heavy hunting pressure. This difference might have resulted from greater interspersion of habitats on Swenson's Box Elder Creek study area, where the 4 habitats preferred by mule deer covered 68% of the area. On Cherry Creek, mule deer selected 5 habitats covering only 32% of the area, and none were available that provided more security than those already being used.

During winter, bunchgrass prairies, badlands, mesic shrublands, and hardwood draws were generally selected; sagebrush grasslands were used in proportion to availability; while mixed prairies, grainfields, and hayfields were generally avoided ($P<0.05$, Table 14). Survey data, which were most representative of habitat use and selection in early winter, may have overestimated preference for mesic shrublands that were used only in proportion to availability by radioed females. Badlands were especially important, accounting for 50% or more of the use measured by both data sets. Badlands and hardwood draws together accounted for 469 (73%) of 640 telemetry locations and 66% of all mule deer observed during surveys; though use of hardwood draws alone decreased in winter as compared to other seasons (Fig. 14). Hardwood draws used by deer were usually located within badlands or bunchgrass prairie; those associated with other habitats were largely unavailable because they filled with drifted snow.

Over all seasons and years, mule deer generally used sagebrush grasslands, bunchgrass prairies, badlands, mesic shrublands, and hardwood draws more than expected on the basis of relative availability (Table 14). Legume hayfields also appeared to be selected, at least seasonally. Mixed prairies and grainfields received less use than expected ($P<0.05$). Mixed prairie and grainfields were characteristic of extensive, level to rolling grasslands that provide little habitat for plains mule deer. Conversely, selected habitats were characteristically associated with rougher terrain that provides excellent mule deer habitat throughout the Great Plains (Severson 1981).

Habitat - Use Relationships

Analyses of habitat characteristics among 25-ha cells used by radio-collared female mule deer identified interactions between habitat resources and patterns of

Table 15. Differences ($P<0.05$) in habitat characteristics of 25-ha grid cells occupied by different migration classes of mule deer during summer and winter on the Cherry Creek area, 1983-1985.

Season	No. of cells	Habitat characteristic	Difference & direction
Winter	308	Area of sagebrush grasslands	SM > AM & YR[a]
		Area of hardwood draws	SM < AM & YR
		Edge of mesic shrublands	SM > AM & YR
		Edge of hardwood draws	AM > SM & YR
Summer	310	Area of badlands	SM < AM < YR
		Area of hardwood draws	SM < AM & YR
		Area of mixed prairies	SM > AM & YR
		Edge of badlands	SM & AM < YR
		Edge of hardwood draws	SM < AM & YR
		Edge of mesic shrublands	SM > AM & YR

[a] SM=summer migrant, AM=autumn migrant, YR=yearlong resident.

habitat selection, distribution, movements, and home range size. Presumably, differences in basic movement patterns among females, intensity of use of local areas, and home range size are all related to differences in the types, juxtaposition, and abundance of habitat resources available to or used by deer.

As expected, yearlong residents, summer migrants, and autumn migrants occupied different ($P<0.05$) habitat complexes, seasonally and overall (Tables 15 and 16). Resident females occupied the same home ranges and used essentially the same habitats yearlong. There were no significant differences in habitat characteristics of cells that these deer used during summer and winter. Areas occupied during both seasons were characterized by badlands with interspersed hardwood draws and other mesic habitats that apparently met their forage and shelter needs throughout the year.

Ranges occupied by summer migrants from December through March contained significantly less hardwood draw habitat, more sagebrush grassland and more mesic shrubland edge than those used by residents or autumn migrants (Table 15). These differences indicated that summer migrants occupied winter ranges that were

Table 16. Differences (*P*<0.05) in habitat characteristics of 25-ha grid cells occupied in summer and winter for each migration class of mule deer on the Cherry Creek area, 1983-1985.

Migration class[a]	No. of cells	Habitat characteristic	Difference & direction
SM	224	Area of mixed prairies	summer > winter
		Area of sagebrush grasslands	summer > winter
		Area of bunchgrass prairies	summer < winter
		Area of badlands	summer < winter
		Area of mesic shrublands	summer > winter
AM	149	Area of sagebrush grasslands	summer > winter
		Edge of bunchgrass prairies	summer < winter
YR	235	No seasonal differences	

[a] SM=summer migrant, AM=autumn migrant, YR=yearlong resident.

comparatively drier than those occupied by other segments of the mule deer population. This apparently influenced both early migration and patterns of habitat use throughout the year.

In spring, summer migrants moved to summer ranges that contained less badland and bunchgrass prairie and more mixed prairie, sagebrush grassland, and mesic shrubland habitat than their winter range (Table 16). These summer ranges also had less area in hardwood draws and more mesic shrubland edge than those occupied by residents and autumn migrants. Although this complex was somewhat more mesic than that used during winter, it remained a relatively dry environment that apparently provided sufficient resources only through use of a variety of habitats and relatively large home ranges.

Legume hayfields appeared to be an important component in the habitat of summer migrants. Spotlight counts during 1983 indicated deer use of alfalfa fields increased through summer and peaked in early September (Fig. 15) when 185 deer (4.3/ha) were counted. This count represented 88% of all deer observed within 2 km of the fields during the subsequent autumn aerial survey. Reduced use of fields during late summer 1984 may have been related to drought conditions that reduced growth of alfalfa to the extent that only 3 of 7 fields were cut for hay; all were mowed and produced some regrowth during the summer of 1983.

Areas occupied by autumn migrants from early winter to late summer were most

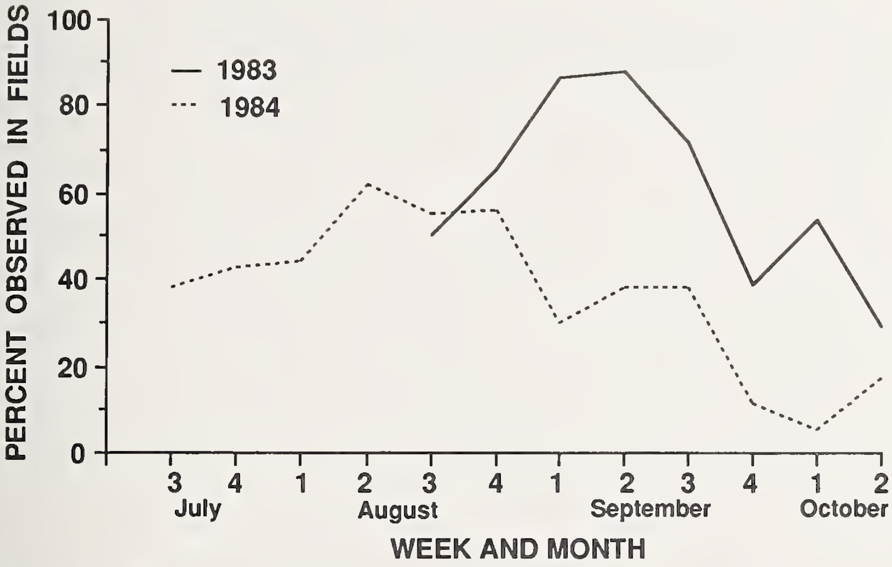


Fig. 15. Alfalfa field use by mule deer and white-tailed deer on the Cherry Creek area during July-October, 1983 and 1984. Data are percent of total deer counted in the drainage during autumn aerial survey that were observed during weekly spotlight counts.

similar to those occupied by yearlong residents. Cells used by autumn migrants during summer contained significantly less badlands area and edge than those used by the resident segment (Table 15). However, they were more mesic than those occupied by the summer migrants in that they contained greater area of badlands, greater area and edge of hardwood draws, less area of mixed prairie, and less edge of mesic shrubland.

Although differences in habitat characteristics between areas used by autumn migrants and resident deer were minor, they did influence some differences in habitat use. Cells used by autumn migrants during summer contained greater area of sagebrush grassland and less edge of bunchgrass prairie than cells used during winter (Table 16). Thus, autumn migrants, like summer migrants, may have compensated for reduced area of badlands or other habitat deficiencies within their home ranges by using a greater variety of habitats to meet their resource needs. It was only during late summer and autumn, when those needs could not be met on ranges occupied during the remainder of the year, that they moved to alternate ranges.

Habitat characteristics associated with areas (grid cells) receiving relatively high and low use by radio-collared females are listed in Table 17. Variables significantly influencing intensity of use differed between summer and winter, and among residents, autumn migrants, and summer migrants.

During winter, cells used intensively by yearlong residents contained more badlands habitat than those receiving only light use ($P<0.05$). Cells used intensively by summer migrants contained more badlands, less mixed prairies, and less diversity ($P<0.05$) as compared to cells used less intensively. Autumn migrants exhibited more intense use of cells with more bunchgrass prairies and less mixed prairies. Thus, badland and/or bunchgrass prairie habitats were important components of winter range for all mule deer. Bunchgrass prairie apparently provided suitable winter habitat if

Table 17. Differences ($P<0.05$) in habitat characteristics of 25-ha grid cells occupied at high (≥ 3 observations/cell) and low (1 observation/cell) intensity for each migration class of mule deer on the Cherry Creek area, 1983-1985.

Migration class[a]	No. of cells	Habitat characteristic	Difference & direction
		Winter	
SM	103	Area of mixed prairies	low > high
		Area of badlands	low < high
		Diversity index	low > high
AM	53	Area of mixed prairies	low > high
		Area of bunchgrass prairies	low < high
YR	92	Area of badlands	low < high
		Summer	
SM	80	Area of sagebrush grasslands	low < high
		Edge of hardwood draws	low < high
AM	65	Area of mixed prairies	low > high
YR	98	Area of badlands	low < high

[a] SM=summer migrant, AM=autumn migrant, YR=yearlong resident.

abundant or interspersed within badlands.

Areas used intensively by yearlong residents during summer also contained greater area of badlands than low use areas ($P<0.03$). Autumn migrants showed a similar pattern, though the only significant difference was a decrease in amount of mixed prairie ($P<0.007$) in high-use cells. Both results manifest the importance of badlands for summer range because the study area was dominated by badlands and mixed prairies. Cells used intensively by summer migrants contained significantly

Table 18. Differences ($P<0.05$) in habitat characteristics of 25-ha grid cells occupied by mule deer with the 5 largest and 5 smallest home ranges on the Cherry Creek area, 1983-1985.

Season	No. of cells	Habitat characteristic	Difference & direction
Winter	131	Area of mixed prairies	large > small
		Area of badlands	large < small
		Area of hardwood draws	large < small
		Diversity index	large > small
Summer	149	Area of mixed prairies	large > small
		Area of sagebrush grasslands	large > small
		Area of badlands	large < small
		Area of hardwood draws	large < small
		Edge of hardwood draws	large < small

more sagebrush grassland and interspersed hardwood draw edge than low use areas. Hardwood draws, an important component of summer habitat for all deer, were relatively scarce within ranges of summer migrants. Thus, these deer tended to concentrate in and around those draws that were available.

Habitat features that influenced differences in movement patterns and intensity of mule deer use on the area also influenced home range size (Table 18). During winter, smaller home ranges were associated with increased area of badland and hardwood draw habitat, less mixed prairie, and lower diversity indices ($P<0.05$). Deer apparently compensated for a lack of badlands and hardwood draws on their winter range by increasing home range size and by using a variety of other habitats as indicated by an increased diversity index within cells occupied by deer with larger home ranges.

Differences in habitat characteristics ($P<0.05$) between cells occupied by deer with large and small home ranges in summer illustrated that the badlands-hardwood draw complex was important in habitat use throughout the year. Deer ranged over larger areas that included more sagebrush grassland and mixed prairie habitat when badlands and hardwood draws were less abundant.

Collectively, these findings indicate that patterns of distribution, movement, home range size, and habitat selection reflect behavioral responses of mule deer to environmental features available to them. This tends to confirm the importance of resource distribution on movement patterns of mule deer as reported by Eberhart et al. (1984) and Severson and Carter (1978). Results also support the conclusion of Severson and Carter (1978:467) that "rougher terrain and more extensive cover types apparently allowed . . . deer to fulfill requirements in smaller areas".

During winter, the availability of badlands appeared to be a major factor influencing mule deer distribution and habitat use. Badlands habitat dominated areas used as winter range, comprised 44% of the area of 25-ha cells occupied by radio-collared females from December through March, and was highly selected. Other habitats were used largely as a result of their association or interspersion with badlands. The steep, rugged topography of badlands apparently served to ameliorate environmental conditions by providing shelter from the wind (Wood 1988), preferred forage, and minimum snow depths.

Interspersion of suitable hardwood draws and badlands on Cherry Creek seemed to provide all resources required by mule deer throughout the year, resulting in yearlong residency. It also resulted in smaller home ranges and higher local deer densities. When badlands and hardwood draws were lacking or more widely separated, deer used combinations of other habitats, ranged over larger areas, and occurred at lower densities.

During summer, mule deer were more widely dispersed and exhibited greater variability in habitat use than during winter. Summer habitat use patterns were directly influenced by the types, amounts, and distribution of resources available throughout the year. Availability of succulent green forage, that is usually limited in this semiarid environment, was particularly important, especially during late summer and autumn. Late summer movements observed during this study probably reflected shifts to areas with more succulent forage as reported in other plains habitats (Martinka 1968, Mackie 1970, Dusek 1975).

Other investigators (Dusek 1975, Swenson, unpubl. rep., Mont. Fish and Game, 1978, and Steigers 1981) have reported greater use of grassland habitats by mule deer than observed during this study. However, a careful review of these reports indicated that this difference was largely a reflection of how habitats were defined and mapped in the various studies (Wood 1987). The high degree of avoidance of mixed prairie by mule deer on our study area did not indicate an intrinsic avoidance of "grasslands", but rather, that needs for topographic relief and/or forage were not met in that habitat. Habitats capable of supporting mule deer in prairie environments can be very limited in their distribution and abundance. Any that provide both cover and forage throughout the year are probably suitable regardless of what plant species dominate.

White-Tailed Deer

Distribution

White-tailed deer generally occurred in more scattered, lower density aggregations than mule deer. They were observed in only 19% of the 25-ha grid cells during aerial surveys from 1975 through 1986. Only 8% of the cells were occupied in autumn, 11% in winter, and 7% in spring. Areas of concentration appeared to change somewhat during the study, but overall spatial distribution remained essentially

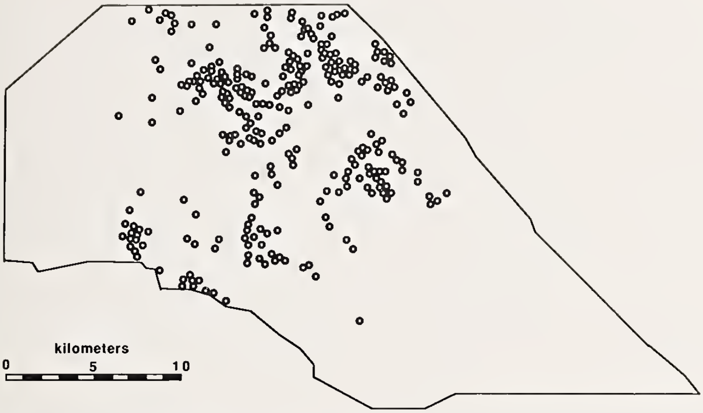


Fig. 16. Distribution of white-tailed deer groups observed on the Cherry Creek study area during aerial surveys in winter, 1975-1985.

unchanged from 1975 through 1986. Whitetails occupied and avoided the same 25-ha cells during both early (1975-1979) and later (1982-1986) years of the study ($P<0.001$).

The general pattern of dispersion based on distribution of whitetail groups observed during winter surveys from 1975 through 1985 is shown in Figure 16. Greatest concentration and most continuous distribution were found within a block extending northeast from the headwaters of Cherry Creek in the southwest corner, across Big Sheep Mountain to the northern boundary of the area. This included middle to upper portions of second- and third-order drainages and interspersed rangeland where riparian and agricultural habitats predominanted. Within this general distribution, local concentrations were interspersed among areas where white-tailed deer were absent or occurred in extremely low densities.

Concentration areas seemed to differ between sexes. The number of mature males observed/cell during a single summer or autumn survey was negatively correlated with the number of adult females ($r_s=-0.38$, $P<0.001$) and the number of fawns ($r_s=-0.63$, $P<0.001$). Numbers of fawns and females observed/cell were not correlated ($P>0.2$).

Whitetail aggregations did not comprise distinct subpopulations within the study area. The only consistent associations occurred between a doe and her offspring of the previous 1-2 years, as described by Hawkins and Klimstra (1970) and Nelson and Mech (1987). High emigration rates of young deer and occasional shifts in the location of large home ranges caused an interweaving of individual home ranges and apparently precluded development of large matrilineal groups using traditional seasonal ranges.

Movements and Home Range

Overall, 1,979 locations were obtained for 34 marked females. Data were sufficiently detailed to identify movement patterns of 24 (16 radioed) during 1983-1984. These deer did not exhibit discrete movement patterns (i.e., yearlong residency, summer and autumn migration) like mule deer. Tests for differences in AARs due to collar type (radio or neckband), migration class, and months, showed a significant difference in movements only among months ($P<0.05$). A plot of AARs for all female

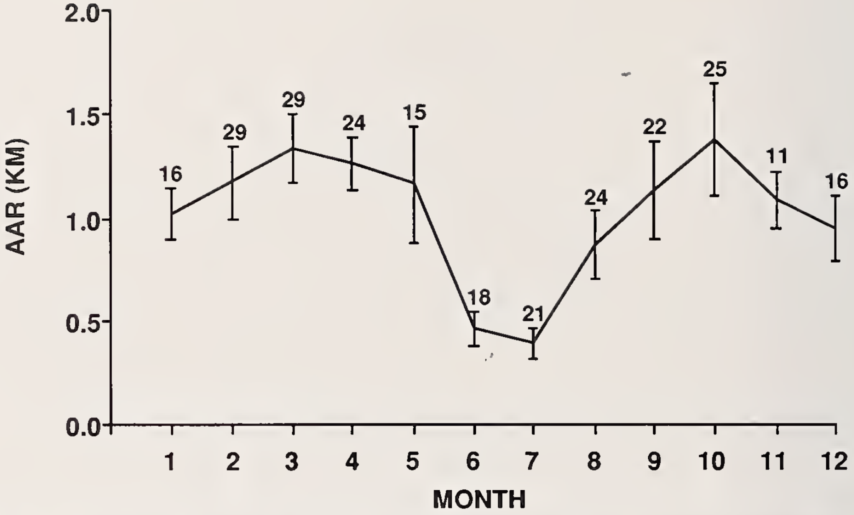


Fig. 17. Monthly average activity radius (mean ± SE) for female white-tailed deer on the Cherry Creek area, 1983-1985. Numbers of deer are recorded above each point.

whitetails (Fig. 17) revealed relatively large movements during all months except June and July. More importantly, monthly AARs varied widely among individuals. All of this indicated that each whitetail developed a unique pattern of home range use and movements in response to the distribution of resources available to it.

During 1983 and 1984, eleven (46%) of 24 females occupied home ranges consisting of a variable number of intensively used subareas, as described by Sparrowe and Springer (1970) and Inglis et al. (1979). Eight (33%) moved an average of 6.1 km (range, 3.6-9.6 km) during autumn to areas nearer grainfields. The remaining 5 females (21%) moved between 2 or more distinct ranges at various times of the year. One of these moved between 2 ranges separated by 13 km; the northern range was used during spring, the southern during summer, and either during autumn and winter. Another occupied 3 distinct ranges; an autumn range (Aug-Nov), a winter range (Dec-Apr), and an intermediate fawning range (May-Jul). Distance from fawning to autumn range was 4.5 km, that from autumn to winter range was 13.2 km, and that from fawning to winter range was 8.7 km. The other 3 used 1 range during spring and autumn and another during summer and winter.

Female white-tailed deer exhibited individual patterns of movement that ranged from relatively small, stable home ranges to erratic shifts within very large home ranges. Study-long AARs varied from 0.65 to 5.45 km; polygons ranged from 3.5 to 80.3 km^2 (Table 19). In contrast to mule deer, individual whitetails occupied smaller ($P<0.02$) ranges during summer than winter.

Home ranges of white-tailed deer on Cherry Creek generally were larger than those reported for other environments. Winter home range size on Cherry Creek (6.3 km^2) was most similar to home range size in eastern South Dakota (4.6 km^2, Sparrowe and Springer 1970), and southern New Brunswick (3.3 km^2, Drolet 1976). Summer home range size (3.3 km^2) was most similar to southeastern Montana (3.8 km^2, Dusek 1987) and eastern South Dakota (2.6 km^2, Sparrowe and Springer 1970).

Table 19. Estimated average activity radius (AAR) and polygon home range size for female white-tailed deer on the Cherry Creek area, 1983-1985.

		No. points/ Home range		AAR (km)			Polygon (km^2)		
Season	No. deer	$\bar{X}$	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range
Study-long	15	50	24-73	2.12	0.31	0.65-5.45	33.48	6.22	3.51-80.28
Summer	19	15	10-19	0.92	0.09	0.35-1.49	3.26	0.56	0.42-8.81
Winter	17	15	10-24	1.19	0.10	0.46-1.73	6.34	1.06	1.12-13.70

Emigration and Home Range Fidelity

As noted earlier, the incidence of emigration by white-tailed deer appeared relatively high. All 4 marked male fawns were believed to have left the study area as yearlings based on the time and pattern of their disappearance, and 3 of 5 females collared as fawns were known to have emigrated. No males were relocated. One of the 3 emigrating females was consistently observed on the area until 3 years of age, then disappeared. She was shot by a hunter 2 years later 93 km east of her ancestral range. Another was observed regularly with a radioed female through summer, disappeared as a yearling in October, and was found dead (an apparent roadkill) 51 km southeast of her last known location during the following May . The third disappeared in March, when approximately 9 months old, and was relocated the following January and 3 times thereafter through November on what may have been a new home range 12 km southwest of her natal range.

Although no females $\geq$4 years of age emigrated, movement patterns of whitetails generally were typified by a high degree of mobility and erratic seasonal shifts of their home ranges. Mature females often used the same general area for fawning from year to year, but exhibited little fidelity to other range areas. Six of 15 marked females observed for >2 years used different seasonal ranges between consecutive years. These deer made unpredictable shifts within their study-long home range and did not seem to establish permanent home ranges.

Habitat Selection

Patterns of habitat use and selection based on data from aerial surveys throughout the study and telemetry relocations during 1983-1985 were generally similar with respect to use of most major habitats (Table 20). Contradictions involving use of sagebrush grasslands probably were an artifact of the distribution of radioed females in the population. Sagebrush grasslands were heavily used by whitetails occupying the south-central portion of the study area where there were no radioed deer. Differences in seasonal and annual preference for bunchgrass prairie appeared related to sample size; generally, the larger sample of deer observed during surveys was sufficient to

Table 20. Habitat use of white-tailed deer on the Cherry Creek study area based on radio locations (1983-1985) and deer observed during aerial surveys (1975-1985). Data are percentage of observations occurring in each cover type and a selection coefficient indicating avoidance (A) or selection (S) ($P<0.05$), or use in proportion to availability (U) ($P>0.05$). No pattern is indicated (A, S, or U) if insufficient data were available for test.

	Annual		Spring		Summer		Autumn		Winter	
Habitat	Radio	Survey	Radio	Survey	Radio	Survey	Radio	Survey	Radio	Survey
Mixed prairies	12 A	16 A	8 A	16 A	9 A	11 A	16 A	13 A	16 A	17 A
Grainfields	7 U	12 S	3 U	18 S	3 U	2 A	12 S	16 S	8 U	5 S
Hayfields	2 U	2 S	4	2 S	2	13 S	2	5 S	1	0 U
Sagebrush grasslands	2 A	5 S	0	6 U	2 U	12 S	2 U	8 S	3 U	4 U
Bunchgrass prairies	8 U	10 S	15 U	13 S	4 U	0 A	5 U	3 A	9 U	11 S
Badlands	0 A	7 A	0 A	5 A	0 A	0 A	1 A	1 A	1 A	11 A
Mesic shrublands	8 S	6 S	8 S	5 S	9 S	23 S	14 S	16 S	2 U	2 U
Hardwood draws	61 S	42 S	62 S	35 S	71 S	39 S	48 S	38 S	60 S	50 S
Total Observations	641	3,021	112	986	180	187	133	664	216	1,186

show selection or avoidance ($P<0.05$) where smaller samples of radio data did not.

Both sample size and distribution of radioed deer probably contributed to differences in patterns of use and selection for hayfields and grainfields; both habitats had limited distribution on the area. Some differences such as consistently greater use of hardwood draws by radioed deer apparently were influenced by differential visibility of deer among habitats. However, there was no difference in average group size of deer observed during aerial surveys, as compared to radio-located groups during any season ($P>0.05$).

During spring, whitetails selected hardwood draw, mesic shrubland, and hayfield habitats; they avoided badlands and mixed prairies. Bunchgrass prairies and grainfields also appeared to be selected, at least in early spring, though radioed females used both in proportion to availability (Table 20). Hardwood draws were most heavily used and highly selected, while bunchgrass prairie received greater use during spring than other seasons in both data sets.

In summer, hardwood draw, mesic shrubland, legume hayfield, and sagebrush grassland habitats were selected; badlands, bunchgrass prairies, grainfields received very little use and were avoided. Mixed prairies received moderate use, but overall were avoided. Hardwood draws and mesic shrublands were both heavily used, collectively accounting for 62% of all deer observed during aerial surveys and 80% of all radio locations in summer. Use of hardwood draws was greatest during June (Fig. 18). As with mule deer, use and importance of legume hayfields varied between summers 1983 and 1984 and may have been underestimated due to sampling bias.

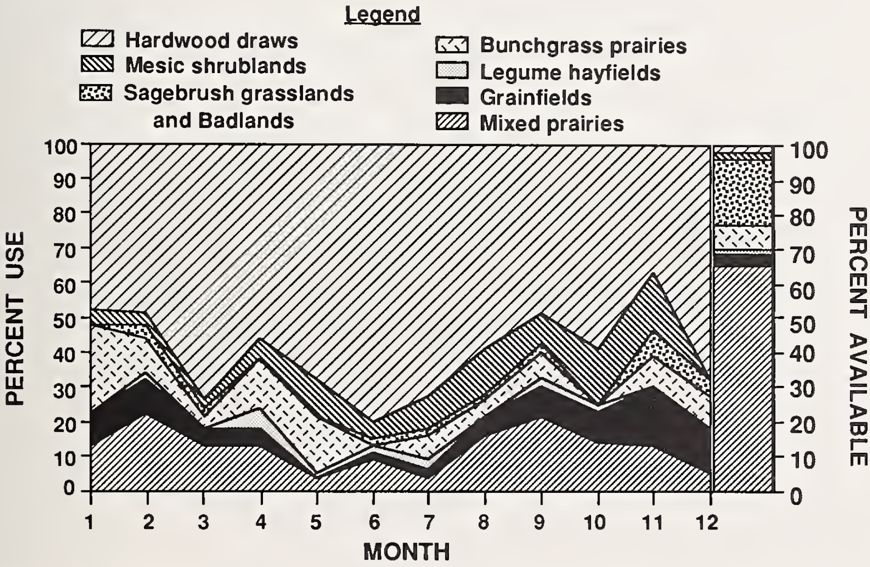


Fig. 18. Monthly patterns of habitat use by radioed female white-tailed deer on the Cherry Creek area, 1983-1985, relative to habitat availability.

Habitat use and selection during autumn generally followed that for summer (Table 20), except that grainfields received increased use and were highly selected. This autumn shift to grainfields was the most significant change in habitat use by white-tailed deer through the year, and reflected movement of many deer to harvested fields to feed on waste grain. It involved large shifts in centers of activity and increased home range size among radioed females. Overall, hardwood draws continued to receive heaviest use; mesic shrublands received moderate use and were selected. Although sagebrush grasslands and legume hayfields also were selected, use of both was relatively minor. Mixed prairies, which received moderate use, bunchgrass prairies, and badlands were generally avoided.

During winter, whitetails heavily and selectively used hardwood draws (Table 20). Bunchgrass prairies and grainfields also appeared to be generally selected. Use of mesic shrublands and sagebrush grasslands was only in proportion to availability. Mixed prairies and badlands were avoided, though both received moderate use. Legume hayfields appeared to be used only rarely in winter.

On a yearlong basis, whitetails most heavily used and selected hardwood draws (Table 20). Mesic shrublands were selected during all but winter. Bunchgrass prairies, sagebrush grasslands, grainfields, and legume hayfields also may have been generally selected, though small samples of data for radioed females indicated random use or avoidance. Badlands and mixed prairies were avoided. Although the latter ranked second to hardwood draws in yearlong use, it covered approximately 65% of the study area.

Habitat - Use Relationships

Female white-tailed deer were similar to yearlong resident mule deer in that areas (25-ha grid cells) in which they occurred during summer were not different ($P>0.05$) from those occupied during winter. Extensive movement and large individual home ranges apparently allowed whitetails to select habitats that met all of their seasonal forage and other resource needs within the same general area.

Analysis of habitat characteristics among 25-ha grid cells used by radio-collared females with relatively large and small home ranges and at relatively high (≥ 3 observations/cell) and low (1 observation/cell) intensities indicated that spatial distribution, movements, and home range size of whitetails, like mule deer, were significantly influenced by the types, amounts, and juxtaposition of habitats available. Both composition and diversity of habitat complexes appeared to be important.

Areas of intensive use during summer comprised more diverse habitat complexes with greater area of legume hayfield than those of low use ($P<0.05$) (Table 21). More diverse habitat complexes also were associated with higher deer density or intensity of use during winter.

Table 21. Differences ($P<0.05$) in habitat characteristics of 25-ha grid cells occupied at high (≥ 3 observations/cell) and low (1 observation/cell) intensity by whitetails on the Cherry Creek area, 1983-1985.

Season	No. of cells	Habitat characteristic	Difference & direction
Summer	72	Diversity index	low < high
		Area of hayfields	low < high
Winter	66	Diversity index	low < high

During summer, females with smaller home ranges used cells having greater area of hardwood draw, less area of mixed prairie and grainfields, greater area and edge of legume hayfield, greater edge of bunchgrass prairie, and less edge of mesic shrubland than cells used by females with larger home ranges ($P<0.05$) (Table 22). Use of

Table 22. Differences ($P<0.05$) in habitat characteristics of 25-ha grid cells occupied by whitetails with the 5 largest and 5 smallest home ranges on the Cherry Creek area, 1983-1985.

Season	No. of cells	Habitat characteristic	Difference & direction
Summer	105	Area of mixed prairies	large > small
		Area of grainfields	large > small
		Area of hayfields	large < small
		Area of hardwood draws	large < small
		Edge of hayfields	large < small
		Edge of bunchgrass prairies	large < small
		Edge of mesic shrublands	large > small
Winter	129	Area of mixed prairies	large > small
		Area of grainfields	large > small
		Area of hardwood draws	large < small
		Edge of badlands	large < small
		Edge of mesic shrublands	large > small

grainfields increased home range size because these fields were larger than legume hayfields and were surrounded by mixed prairie and associated mesic shrublands or sagebrush grasslands in adjacent drainages. Such habitat complexes were generally drier than those associated with legume hayfields, hardwood draws, and bunchgrass prairies.

Poor interspersion of preferred cover and forage areas caused deer to travel farther between feeding and bedding areas, thus increasing home range size. This influence of habitat interspersion on movements of white-tailed deer also was observed by Carlsen and Farmes (1957), who reported that deer ranged more widely in relatively open prairie-deciduous forest habitats as compared to denser coniferous forests. Larger home ranges are apparently an attempt to effectively use areas where preferred habitats occur in widely scattered patches.

Increased area in grainfields and mixed prairies, and increased edge of mesic shrublands also increased deer movements and home range sizes during winter (Table 22). Hardwood draws interspersed among badlands resulted in decreased home range size even though whitetails were rarely observed directly using the badlands.

The importance of habitat diversity to white-tailed deer during winter contrasted with findings for mule deer, but was consistent with whitetail habitat relationships in other areas of eastern Montana (Dusek et al. 1988, 1989). White-tailed deer in the northern Great Plains apparently require a diversity of habitats to provide for their needs throughout the year.

During mild winters or periods of little snow cover, whitetails moved widely and used a variety of habitats. During more severe weather, they concentrated in and around hardwood draws interspersed among badlands, apparently for increased shelter. Rongstad and Tester (1969) reported that white-tailed deer exhibited a shelter seeking response, when snow depths exceeded 25 cm. Use of badlands could minimize effects of snow accumulation on whitetails in the same way as for mule deer (Wood 1988), though whitetails seem to prefer areas of more gentle terrain (Hudson et al. 1976, Swenson et al. 1983). This could explain the importance of diversity and hardwood draws in habitat complexes used intensively by whitetails on the area.

Habitat complexes consisting of interspersed hardwood draws, bunchgrass prairie, and agricultural fields provided suitable yearlong habitat for both species. *(Photo by: Ed Brye, Courtesy of North Dakota Game and Fish Department)*

The importance of winter ranges that provided suitable shelter was illustrated by movements of 4 radioed females during February and March 1983. Warm weather melted snow cover during February 1983. In response to these spring-like conditions, all 4 deer moved 6-8 km to areas they used during spring and autumn that were dominated by mixed prairies and grainfields. A snowstorm on March 6 that deposited 10 cm of snow caused them all to return to their normal winter range that contained badlands interspersed with hardwood draws.

Others (Allen 1968, Martinka 1968, Zwank et al. 1979, Dusek 1987) have observed a preference by whitetails for overhead tree cover during winter, presumably to conserve energy. However, Moen (1966) and Kramer (1971) reported that whitetails may use open habitats rather than adjacent tree cover if high energy forages are available to compensate for energy losses resulting from increased exposure to environmental extremes. Our findings suggest that white-tailed deer in plains environments may follow either strategy of habitat use as winter conditions change. With light snow cover, they were mobile, feeding in agricultural fields and bedding in adjacent drainages. When snow depths increased and temperatures dropped, they conserved energy by moving to more protected areas and utilizing native forages available within the badlands-hardwood draw complex. Drolet (1976) reported similar responses by whitetails to changing environmental conditions in New Brunswick.

Both riparian and agricultural habitats appeared to be key components influencing distribution and habitat use of white-tailed deer. Hardwood draws, which comprised the principle riparian habitat, were heavily used and selected during all seasons. Their interspersion with agricultural and other habitats directly influenced seasonal deer distribution, movements, and home range size.

Whitetails also seemed dependent on agricultural crops, as indicated by habitat use patterns. All marked whitetails made some use of agricultural fields, as compared to only 25% of 96 marked female mule deer. Deer normally restrict forage intake and utilize stored fat reserves during winter even when provided with unlimited supplies of high quality forage (Thompson et al. 1973). Use of agricultural crops throughout the year might provide energy reserves necessary for overwinter survival of whitetails in prairie environments.

COMPARATIVE ECOLOGY

Population trends of mule deer and white-tailed deer were similar but the magnitudes of change differed. Populations of both species increased from 1976 to peak densities in spring 1983 and 1984, and both declined through 1986. However, mule deer increases during 1976-1983 were larger than those of whitetails because whitetails exhibited no consistent increases until after 1980. The ratio of whitetails to mule deer was 111:100 during spring 1976, dropped to 42:100 by spring 1980, and 31:100 by spring 1983. Subsequent declines were greater for whitetails such that by spring 1987 the ratio had dropped to 9:100.

Fawn production, estimated by recruitment to autumn and early winter, appeared to be relatively high and similar for both species. Field classifications during 11 years indicated that mule deer recruited an average of 73 fawns:100 females during autumn, while white-tailed deer recruited 77:100. In early winter, mean ratios were 72 fawns:100 females for mule deer and and 74:100 for whitetails. Although recruitment varied seasonally and among years, there were no consistent differences between the 2 species. Recruitment by mule deer to autumn exceeded that for whitetails by 10 or more fawns:100 females during 4 years, was lower in 4 years, and about equal in 3 years. In early winter, mule deer recruited more fawns in 3 years, fewer in 4 years, and essentially the same number in 4 years.

Fawn production and recruitment in both species was directly correlated with total precipitation from July through April preceding fawning. Thus, the 2 species also responded similarly to favorable conditions that prevailed from 1978-1982 and unfavorable drought conditions that prevailed during 1983-1985. Interaction between population and environmental factors resulted in somewhat different seasonal recruitment patterns for the 2 populations in any given year. Collectively, these data confirm Beasom and Wiggers (1984) conclusion that there apparently is no inherent difference in potential productivity between the 2 species.

During 1983-1986, mortality rates of whitetail fawns were higher during summer and autumn (65% and 32%, respectively) than those of mule deer fawns (41% and 21%, respectively), but overwinter mortality was much lower for whitetails (12% vs. 43%). This resulted in annual mortality rates of 82% for whitetail fawns compared to 70% for mule deer fawns. Fawn:doe ratios during spring did not differ across all years ($t = 0.02$, $P > 0.3$) or between individual years (paired-sample $t = 0.06$, $P > 0.3$). This supported the conclusion that net recruitment rates were generally similar for the two species populations. Thus, differences in species population size during 1980-1986 must have resulted from differences in adult mortality or emigration rates.

Average annual rates of population decline from 1982 to 1987, excluding the hunting season, were higher for adult male whitetails than for adult female whitetails or adult mule deer of either sex ($P < 0.05$). No other rates of decline were statistically different, but there was a consistent pattern of higher rates for whitetails during summer. White-tailed deer populations declined an average 26% for adult males and 9% for adult females during summer (Table 8), whereas mule deer declines averaged 3% for males and 1% for females (Table 4). Maximum declines for females during summer also were greater for whitetails (16 vs. 3%). Average losses during winter were low for adults of both species, ranging from 0 to 12%. Rates of population decline during summer were generally higher at higher population densities for both species, suggesting a possible density-dependent response in emigration and/or mortality rates. The whitetail population seemed to experience a higher and more variable rate of turnover than mule deer throughout this study.

Mortality rates of adults during hunting season were variable and influenced by hunting regulations. It is widely believed that whitetails are less vulnerable to hunters than mule deer where the species are sympatric (Kramer 1972). Our data suggested this may be true among males, but apparently not among females. During 1982 and 1983 when hunting permits were valid for either species, females of both species experienced similar rates of harvest, whereas male harvest rates were higher for mule deer (Table 23). The liberal regulations designed to encourage the harvest of antlerless whitetails during 1984 and 1985 increased harvest rates for both sexes but proportionately more for females than males.

Table 23. Harvest rates for adult male and female mule deer and white-tailed deer on the Cherry Creek area, 1982-1985. Data are percentage of preseason population that disappeared from the area during the hunting season.

	Mule deer		White-tailed deer	
Year	Females	Males	Females	Males
1982	1	62	3	17
1983	9	59	9	1
1984	37	65	60	55
1985	27	48	52	50

Whitetail densities were much lower than those observed for mule deer after 1980. White-tailed deer also occurred in more scattered aggregations and used less of the area. Winter whitetail density peaked at 0.6/km^2 during December 1982 compared to a peak of 2.3 mule deer/km^2 during December 1983. Whitetail densities varied locally to a maximum of about 5/km^2 whereas, local densities of mule deer generally exceeded 5/km^2, with some reaching 33/km^2.

The limited availability of suitable habitat for both species of deer on the study area increased the potential for spatial overlap. Overall, more than half of the area (54% of all 25-ha grid cells) was not occupied by either species during 1975-1986; 72-87% of the area was not used seasonally. Although some overlap occurred (5-10% of all occupied cells contained both species), distributions of the 2 species were apparently independent because there were no correlations between the number of mule and white-tailed deer per cell either seasonally or annually ($r_s<0.28$, $P>0.30$).

Spatial overlap indices (Table 24) also indicated the 2 species were distributed independently. Spatial overlap was greatest during summer and autumn and least

Table 24. Seasonal overlap indices (Hurlbert 1978) between mule deer and white-tailed deer on the Cherry Creek area, 1982-1987.

	Habitat overlap			Spatial overlap		
Season	L[a]	$Z_{w(m)}$[b]	$Z_{m(w)}$[c]	L	$Z_{w(m)}$	$Z_{m(w)}$
Spring	12.90	2.13	4.98	0.19	0.41	1.32
Summer	17.01	4.51	16.18	0.47	0.34	0.98
Autumn	9.13	1.79	3.10	0.62	0.69	2.98
Winter	7.70	2.45	7.26	0.26	0.62	2.09

[a] L - Combined overlap index.

[b] $Z_{w(m)}$ - Overlap on mule deer by whitetails (whitetails/25 ha).

[c] $Z_{m(w)}$ - Overlap on whitetails by mule deer (mule deer/25 ha).

during winter and spring. Within areas of overlap, mule deer density generally exceeded that of whitetails during all seasons. This was inevitable because mule deer densities were higher than whitetail densities across the area.

There was substantial interspecific overlap in habitat preference and use patterns (Table 24). Both species selected and intensively used limited habitats such as hardwood draws, especially in summer. Both generally avoided use of mixed prairies, which covered about 65% of the study area. Minimum overlap occurred during winter when mule deer predominantly used badlands and made only limited use of hardwood draws, but preferences still coincided. Directional indices of habitat overlap demonstrated that whitetails were potentially more affected by overlap than mule deer.

Despite similar habitat preferences, mule deer and white-tailed deer maintained independent distributions. This indicated that other attributes of habitat use were probably more important than habitat preferences in determining spatial distribution. Whitetails generally were more mobile, followed different movement patterns, and had significantly larger home ranges ($P < 0.01$) both seasonally and annually. Most did not establish and use traditional home ranges, but continually shifted between areas used intensively for a few days to a few weeks. Similar patterns have been reported for both species in other areas (Inglis et al. 1979, Eberhardt et al. 1984).

Patterns of distribution, movement, home range size, and habitat use did not reflect direct relationships between deer and individual habitat components. Rather, they reflected responses of both species to overall habitat complexes that were seasonally important to each. Based on data collected during this study, we constructed a "decision tree" model (Fig. 19) to summarize habitat characteristics that influenced whether prairie areas could be occupied by mule deer, white-tailed deer, or

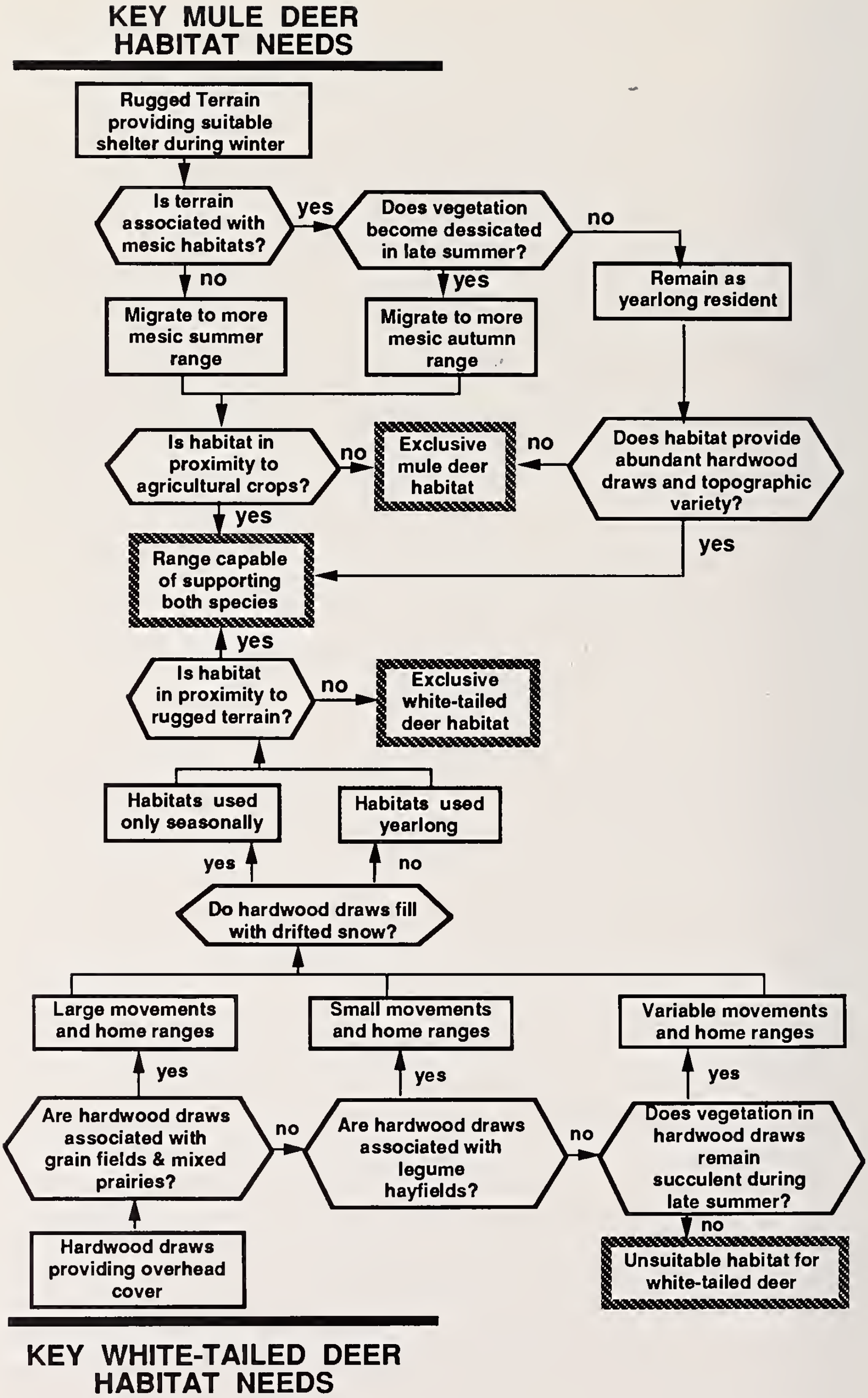

KEY MULE DEER HABITAT NEEDS
Rugged Terrain providing suitable shelter during winter
Is terrain associated with mesic habitats?
yes
Does vegetation become dessicated in late summer?
no
Remain as yearlong resident
no
Migrate to more mesic summer range
yes
Migrate to more mesic autumn range
Is habitat in proximity to agricultural crops?
no
Exclusive mule deer habitat
no
Does habitat provide abundant hardwood draws and topographic variety?
yes
yes
Range capable of supporting both species
yes
Is habitat in proximity to rugged terrain?
no
Exclusive white-tailed deer habitat
Habitats used only seasonally
Habitats used yearlong
yes
no
Do hardwood draws fill with drifted snow?
Large movements and home ranges
Small movements and home ranges
Variable movements and home ranges
yes
yes
yes
Are hardwood draws associated with grain fields & mixed prairies?
no
Are hardwood draws associated with legume hayfields?
no
Does vegetation in hardwood draws remain succulent during late summer?
no
Hardwood draws providing overhead cover
Unsuitable habitat for white-tailed deer
KEY WHITE-TAILED DEER HABITAT NEEDS

Fig. 19. Habitat characteristics influencing movement patterns and relative distribution of mule deer and white-tailed deer on the Cherry Creek area.

both species. The model also indicates how habitat characteristics altered movement patterns, home range size, and habitat use.

Rough terrain is a key component of mule deer habitat throughout the northern Great Plains (Dusek 1975, Severson and Carter 1978, Swenson et al. 1983). Rough terrain that characterized badland and bunchgrass prairie habitats, provided shelter and other resources needed by mule deer during winter (Wood 1988), was a primary factor influencing mule deer distribution and other habitat use patterns during our study.

The occurrence and degree of interspersion of other habitats within badland and bunchgrass prairie areas also was important. Mule deer that occupied diverse winter ranges that include an abundance of hardwood draws and other mesic habitats used the same range yearlong. Those that wintered in badlands-bunchgrass prairie habitats with few hardwood draws left those areas in spring to use more mesic and productive habitat complexes during the remainder of the year, even though more extensive movements and larger home ranges were required. Autumn migrants occupied winter ranges that were generally similar to, but somewhat drier than complexes used by yearlong residents. They apparently met the needs of mule deer during all but late summer and autumn, when autumn migrants shifted to different home ranges that included habitats with better late summer-autumn forage supplies.

Riparian areas are key components of yearlong habitat for whitetails throughout the northern Great Plains (Dusek et al. 1988). This also was the case on our study area where hardwood draws comprised the primary riparian component. However, the total habitat complex and the extent to which hardwood draws were interspersed among other habitats, especially other mesic and/or agricultural types, also was important (Fig. 19). Thus, hardwood draws associated with grainfields resulted in larger home ranges, whereas those associated with legume hayfields resulted in smaller home ranges. Hardwood draw-agricultural complexes that were not associated with areas providing topographic relief generally were not available for use during winter because they filled with drifted snow. Habitat complexes that included more mesic hardwood draws and badlands or bunchgrass prairies apparently were suitable for yearlong use by either white-tailed or mule deer, regardless of whether agricultural fields were included.

Habitat complexes occupied exclusively by mule deer were somewhat different from those occupied only by whitetails. Mule deer habitats contained more badlands, whereas whitetail habitats contained more agricultural fields and hardwood draws (Table 25). Whitetails also made greater use of the gentle terrain in the mixed prairies during autumn and winter. However, whitetails used habitat complexes that included badlands and mule deer used complexes that included significant hardwood draw and agricultural components. As noted above, habitats complexes suitable for yearlong occupancy by mule deer also provided yearlong range for whitetails.

Mule deer declines coincident with increasing whitetail populations through much of eastern Montana have been attributed to increases in the amount of farmland because of the close association between whitetails and agriculture in this region (Swenson et al. 1983). However, mule deer continue to be more abundant and make extensive use of agricultural crops in some areas with intensive agricultural development (Ball 1987, Watts, unpubl. data). Mule deer and white-tailed deer have been locally sympatric in eastern Montana since at least the late 1800s (Guptill 1890, Dillard 1895, Brown and Felton 1955), prior to extensive habitat changes caused by farming or ranching activities. Their food habits are quite similar (Martinka 1968, Kamps 1969) and habitat preferences show substantial overlap.

Given these similarities in food habits and habitat preferences, it becomes difficult to identify factors that influence the degree of spatial segregation in areas of general sympatry. Contrasting habitat preferences are much clearer across their entire range. Whitetail distributions extend farther eastward into the parklands and forests of northern and eastern North America. They also extend farther southward into the tropical shrublands of South America. Mule deer have exclusive domain over much

Table 25. Seasonal differences ($P<0.05$) in habitat composition of 25-ha cells occupied exclusively by mule deer (MD) or whitetails (WT), or jointly by both species (BOTH) on the Cherry Creek Study Area, 1983-1985.

Season	No. of cells	Habitat	Difference & direction
Spring	411	Grainfields	MD & BOTH < WT
		Hardwood draws	MD < BOTH & WT
		Badlands	MD & BOTH > WT
Summer	264	Hayfields	MD < BOTH & WT
		Badlands	MD & BOTH > WT
		Mesic shrublands	MD > BOTH & WT
Autumn	613	Mixed prairies	MD < BOTH < WT
		Grainfields	MD < BOTH & WT
		Hayfields	MD < BOTH & WT
		Badlands	MD > BOTH > WT
		Hardwood draws	MD < WT < BOTH
Winter	503	Mixed prairies	MD & BOTH < WT
		Grainfields	MD & BOTH < WT
		Badlands	MD & BOTH > WT
		Hardwood draws	MD < WT < BOTH

of the desert shrublands of the Great Basin and California (Baker 1984). There is typically segregation into habitats comparable to those described above even in regions such as the northern Great Plains, where their distributions generally overlap. Throughout the species range, mule deer habitats are generally drier, more rugged, and more open, whereas whitetail habitats are more mesic, contain more woody cover, are less rugged, and are more productive (Kramer 1972, Hudson et al. 1976, Geist 1981, Swenson et al. 1983, Wiggers and Beasom 1986).

Predator avoidance mechanisms may be one factor influencing these habitat preferences. Mule deer rely on their bounding gait to negotiate rough terrain and avoid or confuse predators. Whitetails, in contrast, may use their greater speed to outrun predators along trails in the vegetation or across open terrain. They also are more likely to hide in dense cover to avoid detection (Kramer 1972, Geist 1981).

Subtle differences in digestive physiology also may influence habitat preferences and food habits. Klein (1985) presented data suggesting that whitetails may be more selective in their diets and better adapted for utilizing less forage of higher quality. These are certainly not the only 2 factors that help to promote species segregation and may not even be the most important. It is clear that each species must possess distinct morphological, physiological, and behavioral characteristics that shift mule deer toward one end of a habitat spectrum that is more arid and open and whitetails towards the other end that is more wooded and productive.

Areas of sympatry must be located at intermediate positions along such a habitat spectrum. Therefore, the possibility of competitive exclusion can not be ruled out, particularly when food habits and habitat preferences are similar but distributions are distinct (Anthony and Smith 1977). However, it is necessary to show that joint use of a limited resource restricts distribution or population size to prove that interspecific competition is as an important factor in a species' ecology. This may be difficult because the ecological role of competition in variable prairie environments is questionable in comparison to the importance of other factors such as predation, physical disturbance, or environmental variation (Wiens 1977).

It is unlikely that interspecific competition was important on the Cherry Creek area from 1976 to 1982 because both populations increased over this period. Competitive exclusion may have begun to impact distributions and population dynamics as populations peaked, but the duration was very limited because both populations were subsequently reduced by increased harvest rates.

Habitat alterations have been indicated as the major factor influencing changes in the relative distribution and abundance of mule deer and white-tailed deer (Kramer 1972, Swenson et al. 1983, Wiggers and Beasom 1986). But, distributions are just as likely to result from erratic population fluctuations as from interspecific interactions until populations reach some degree of extended stability (Wiens 1977). Opportunities for species-specific management could be used to make either species dominate in areas of sympatry, although relative densities and productivity may vary according to which end of the habitat spectrum any given area most closely approaches. The potential may exist for competition between mule deer and white-tailed deer, but this would only become important if populations saturate the available habitat and remain fairly stable. The variable nature of prairie environments and the over-riding importance of weather patterns on reproduction and mortality rates may limit the duration of habitat saturation and population stability in northern plains habitats such as our study area.

POPULATION - HABITAT RELATIONSHIPS

Individual deer responded to habitat complexes that were available and to seasonal changes in the habitat through movements and adjustments in the size of their home ranges. The observation that differences in home range size generally reflect the distribution and abundance of resources available to an animal (Severson and Carter 1978, Eberhardt et al. 1984) was supported by findings of our study.

Differences in movement patterns or home range size did not seem to influence reproductive success. There were no differences ($P > 0.1$) between fawn recruitment rates, as measured by the percent fawns in spring, between species or among mule deer with different movement patterns (Table 26). Whitetails maintained high fawn recruitment rates despite the fact they had larger home ranges than mule deer. Summer migrant mule deer had larger seasonal home ranges than yearlong resident mule deer but fawn recruitment rates were not statistically different.

Plants differ in their nutritive qualities among sites even within a single species, and deer seem to have an innate ability to select the most nutritious forage available (Julander et al. 1961). Deer on Cherry Creek apparently used behavioral responses, such as increased mobility, to find forage of sufficient quality along with all other necessary resources. They were able to maintain relatively high reproductive rates through use of such site-specific adaptations during most years.

Habitat quality is believed to be reflected in home range size, density, or net productivity. However, crude density, ecological density, and home range size were all highly variable within and between species, whereas productivity was generally similar (Table 26). A more suitable definition of habitat quality is "the product of density, mean individual survival probability, and mean expectation of future offspring" (Van Horne 1983:896). This definition reflects the probability of survival, absolute density, and the ability to support populations through time.

Given this definition of habitat quality, it is difficult to identify individual vegetative or physiographic components that are high or low quality on the Cherry Creek Study Area. Interrelationships among environmental characteristics, habitat complexes, behavioral responses, and population dynamics indicated that deer made subtle adaptations to both short- and long-term environmental variation. Therefore, it is necessary to define habitat quality as the ability of an area, not 1 or 2 key components, to support deer through time. From this perspective, areas occupied by deer in the prairies can be ranked along a conceptual continuum ranging from "reproductive habitat" that provides resources necessary for adult survival and a high probability of reproductive success, to "nonhabitat" that supports essentially no deer. In the middle of this spectrum are "maintenance habitats" that provide the resources necessary for adult survival but not reproduction.

This conceptual continuum could be used to help explain the population dynamics observed during this study. Prairie environments are characterized by variable annual and seasonal weather patterns resulting in variations in the availability of food and cover (Wiens 1977, Mackie 1983) for all species. Deer density in such a highly variable environment should be in a constant state of flux relative to availability of reproductive and maintenance habitats. Environmental variability should be most strongly reflected in variable rates of fawn recruitment because natural mortality rates of adults were relatively low and quite stable on the Cherry Creek area, as they often

Table 26. Population and habitat characteristics in areas occupied by mule deer that were summer migrants (SM), autumn migrants (AM), and yearlong residents (YR), contrasted with characteristics of mule deer (MD) and whitetails (WT) over the entire Cherry Creek study area, 1976-1986.

Characteristic	SM	AM	YR	MD	WT
Area size (km^2)	98	50	27	543	543
Selected habitats (km^2)	37[a]	29	18	178	73
Adults observed/year	65	51	22	232	70
Fawns observed/year	24	22	10	97	32
Percent fawns in spring	27	30	31	29	31
Relative annual density					
Crude density[b]	0.91	1.46	1.19	0.61	0.19
Ecological density[c]	2.41	2.52	1.78	1.85	1.40
Home range size (km^2)					
Summer	2.88	2.08	1.63	2.23	3.26
Winter	3.41	2.32	2.29	2.72	6.34

[a] Total area of all habitats selected during spring.

[b] Mean number of deer observed/year/km^2.

[c] Mean number of deer observed/year/km^2 of selected habitat.

are in other areas (Caughley 1970, McCullough 1979, Hanks 1981, Skogland 1985).

The relationship between environmental variation and population dynamics was reflected in correlations between fawn production and precipitation for both species on the Cherry Creek area. Availability of reproductive habitat was apparently reduced during periods of drought, resulting in decreased fawn survival. Areas that provided reproductive habitat during wet years apparently provided suitable maintenance habitats during dry years because natural mortality rates among adults remained relatively low. Low densities and highly aggregated distributions of both species suggested that large portions of the area consisted of nonhabitat.

Not all areas within prairie habitat provide the resources necessary to achieve high reproductive success in deer. *(Photo by: Wyoming Game and Fish Department)*

Low densities at the start of this study and subsequent population declines at the end made it impossible to conclusively identify natural factors that helped to limit population size. But, findings of other studies can be used to help develop reasonable and testable hypotheses. The concept of forage limited carrying capacity, as determined by population density, has been widely accepted and applied in big game management. However, fawn survival on our study area was influenced by precipitation independently of population density. Fawn survival remained high when there was adequate precipitation even at high densities. Severe winter weather had a variable effect on overwinter fawn survival and little influence on adult survival or subsequent fawn production. Winter ranges on the Cherry Creek area served to ameliorate environmental conditions (Wood 1988) and provided adequate forage for both mule deer and whitetails.

Nutrient availability, as determined by weather patterns not population density, may be one of the most important factor influencing ungulate population dynamics in semiarid environments (Taber and Dasmann 1957, Wehausen et al. 1987, Hamlin and Mackie 1989). Therefore, a series of wet years should result in high production and survival of deer. Productivity of deer populations in prairie habitats can remain relatively high. For example, an unhunted mule deer population in western North Dakota averaged 101 fawns/100 females during autumn 1981-1985 (J. Samuelson,

Contrary to past assumptions, winter habitat and weather conditions generally had less effect on deer numbers and dynamics then summer range conditions. *(Photo by: Alan K. Wood)*

unpubl. data). Dispersal of young deer may help to limit additional increases in prairie deer populations when high densities are achieved and if weather patterns continue to favor fawn survival. This possibility was suggested by the correlation between density and rates of decline for adult female mule deer during summer, and the observation that maximum population declines for whitetails during summer coincided with peak population densities.

High rates of dispersal in other areas also might have influenced population dynamics. Severson and Carter (1978) reported a 50% dispersal rate of yearling females from an unhunted mule deer population that occupied prairie habitat in South Dakota. Robinette (1966) reported a 35% female dispersal rate in a hunted mule deer population with most movement from lightly to heavily hunted areas. Gladfelter (1978) reported a 24% rate of emigration among female whitetails in central Iowa.

Klein and Strandgaard (1972) described a mechanism of population regulation for roe deer (*Capreolus capreolus*) whereby aggression of females trying to defend an area around their young fawns stimulated dispersal and helped to maintain relatively stable populations. They felt that cover was more important in regulating density than food supply. They speculated that this mechanism would not work for *Odocoileus* species in North America because "segments of deer habitat are often more extensive" and "there are no low density areas to absorb the surplus" (Klein and Strandgaard 1972:78).

Prairie habitats are very patchy and do contain large areas of relatively low density that may absorb surpluses. Population densities also may be reduced locally by heavy hunting pressure. Both mule and white-tailed deer females are antagonistic toward other deer during the fawning season. Females with fawns may even prefer isolation throughout the entire year (Wood 1987). All of these characteristics promoted social regulation of roe deer populations (Klein and Strandgaard 1972) and also may apply to deer in prairie habitats. Gavin et al. (1984) and Dusek et al. (1989) have suggested similar patterns of regulation in white-tailed deer.

Based on all available evidence, we hypothesize that variability in precipitation patterns influence herd productivity by influencing forage quality and thereby physical condition of adults and survival of fawns. Fawn recruitment rates may exceed adult mortality rates under favorable environmental conditions and if so, population density would be maintained through social pressures that cause dispersal of young animals. Increased mortality among adult deer in poorer quality habitats may ultimately limit population size over broad areas in the absence of hunting or predation.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Mule deer population estimates on the Cherry Creek Study Area in spring increased from 180 in 1976, to 1,083 in 1983, stabilized during 1983-1984, and declined to 347 by 1987. Annual mortality rates during 1983-1987 averaged 72% for fawns, 25% for adult females, and 61% for adult males. Hunting was the cause of most adult mortality; nonhunting causes were most prevalent among fawns. Population dynamics were not affected by density during any season except among adult females during summer. Fawn survival was related to precipitation patterns. The combined influence of decreased fawn survival and increased adult harvests resulted in population declines.

White-tailed deer populations in spring decreased from 200 in 1976, to about 135 in 1978, then increased to 335 in 1983 and subsequently declined to approximately 30 in 1987. Annual mortality rates during 1983-1986 averaged 82% for fawns, 48% for adult females, and 53% for adult males. Factors influencing whitetail populations were similar to those affecting mule deer, but whitetails also were subject to periodic EHD outbreaks.

Distribution of mule deer remained essentially unchanged throughout the study. Population growth resulted in an increased density of deer within subpopulation units rather than movement into previously unoccupied habitat. Mature males tended to avoid areas used by females with fawns.

Female mule deer exhibited 3 movement patterns. Yearlong residents occupied 1 home range throughout the year. Summer migrants occupied distinct summer and winter home ranges typical of mule deer inhabiting mountain habitats. Autumn migrants remained on 1 home range throughout most of the year, except from late summer to late autumn, when they moved to a different autumn range. There were significant differences in home range size among deer using the 3 movement patterns; home ranges of summer migrants were largest, yearlong residents were smallest, and autumn migrants were intermediate. Seasonal and study-long home ranges were relatively large compared to those reported in the literature. Females demonstrated fidelity to traditional herd ranges.

Mule deer avoided mixed prairies and small grains and selected all other habitats during some season. Selected habitats comprised only 32% of the area. The availability of rugged terrain during winter and mesic feeding sites during summer appeared to be 2 major factors influencing habitat use. Habitat differences across the area resulted in deer adopting different movement patterns to effectively use available resources within their home range. A complex of badlands and hardwood draws met their annual resource needs. Deer seemed to compensate for a lack of these habitats by using a variety of others.

Whitetails generally used and avoided the same area but concentration areas appeared to change through the study. Mature males seemed to avoid areas used by females with fawns. White-tailed deer did not exhibit discrete movement patterns. Both movement patterns and home range sizes were highly variable. Each female appeared to develop a relatively unique pattern of home range use based on the distribution of resources available to her. Females demonstrated little fidelity to a single home range and often made erratic shifts to different home range areas in consecutive years.

Whitetails avoided badlands and mixed prairies and selected all other habitats during some season. Selected habitats comprised only 17% of the area. Agricultural crops were important to whitetails throughout the year. Habitat complexes that included hardwood draws and agricultural fields, particularly legume hayfields, were preferred. Habitat complexes available to whitetails influenced their distribution and home range size.

Mule deer and white-tailed deer maintained independent distributions despite similarities in habitat preferences. It seemed that either species could effectively use the area. The possibility for competitive exclusion of one species by the other can not be ruled out under these conditions. However, the relatively low densities that prevailed probably precluded competition from having a major impact on either population during this study. Opportunities for species specific management could be used to manipulate the relative proportions of mule deer and white-tailed deer in areas of sympatry.

The role of forage-limited carrying capacity, as determined by population density, is questionable for these populations. Precipitation received prior to fawning season was the major factor influencing fawn recruitment rates of both species. Under favorable environmental conditions and in the absence of significant harvests or predation, both populations may tend to stabilize through a mechanism of social interactions that stimulate the dispersal of surplus young deer.

Availability of mesic habitats, particularly during late summer, was an important factor influencing productivity of both species. Quality of mesic habitats was influenced by precipitation patterns and was reflected in correlations between the

With careful management prairie deer populations can provide high quality recreational opportunities. *(Photo by: Mike Aderhold)* amount of precipitation received and percent fawns in winter and spring. However, these findings do not imply a lack of need for habitat management programs in prairie environments. Habitat management plans that protect existing riparian habitats and/or improve the condition of abused riparian habitats should result in direct benefit to local deer populations. Similarly, interspersion of agricultural croplands, particularly legume hayfields, within native rangeland habitats to provide succulent forage during late summer also could be used to improve local deer habitat.

Harvest rates of adults and survival rates of fawns were the two most important factors influencing population dynamics of both species during this study. Both rates were independent of population density. There were no compensatory decreases in natural mortality rates that resulted from increased harvests or lowered density. Numbers of deer harvested were influenced by numbers of permits sold, not population density. Traditional theories of compensatory natural mortality rates in response to increased harvests, and security thresholds that reduce harvest rates as population density declines, were not operational during this study. If such thresholds exist in this environment, they are apparently too low to be useful as management tools.

Deer were extremely vulnerable to hunters in this area. Consequently, different harvest regimes must be applied to maintain deer populations at desired levels. If high density populations are to be maintained, managers must recognize that there is essentially no harvestable surplus produced in some years. In contrast, hunting regulations that concentrate harvests on the adult female segment of the population can be used in situations where lower deer densities are desired.

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